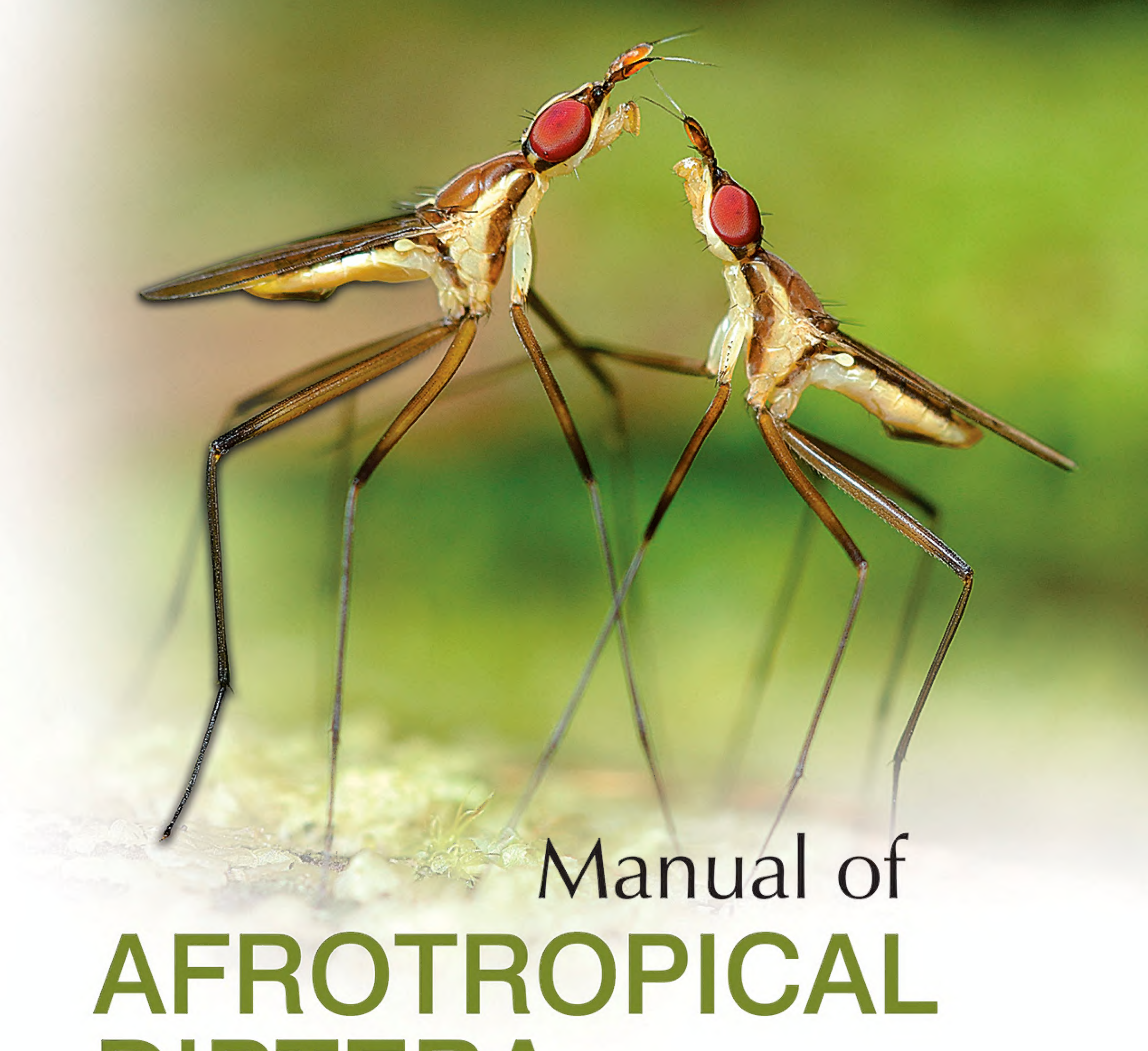

Manual of AFROTROPICAL DIPTERA

Volume 3

Edited by Ashley H. Kirk-Spriggs & Bradley J. Sinclair
With photographs by Stephen A. Marshall

SURICATA 8

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SURICATA 8

Manual of

Afrotropical Diptera

Volume 3

Brachycera–Cyclorrhapha, excluding Calyptratae

Edited by
Ashley H. Kirk-Spriggs & Bradley J. Sinclair

SANBI
Biodiversity for Life
South African National Biodiversity Institute

Pretoria, South Africa
2021

SURICATA

Suricata is the generic name of the suricate (*meerkat*), which is near-endemic to the arid western parts of Southern Africa (occurring in Namibia, South Africa and Botswana; and just entering into a very small area in the extreme south of Angola). Behaviourally, suricates are socially inclusive and innately inquisitive, symbolising the commitment of South African National Biodiversity Institute (SANBI) to include all biodiversity and serve all of Africa and the scientific curiosity that precedes and drives research and publication of research results. Sister journal to SANBI's *Strelitzia*, *Suricata* is a peer-reviewed journal and publishes original and applied research, such as monographs, revisions, checklists, red lists, atlases and faunas of any taxa belonging to Regnum Animalia (the Animal Kingdom).

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DEDICATION

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Volume 3 of the *Manual of Afrotropical Diptera* is dedicated to the memories of the late Amnon Freidberg (1945–2020) (left photo, left), Lloyd Vernon Knutson (1934–2018) (left photo, right) and László Papp (1946–2021) (right photo), who passed away during preparation of this volume. Amnon was a member of our Editorial Panel and was author or co-author on three included chapters (71. Tephritidae, 89. Neminidae and 92. Asteiidae), Lloyd Knutson was co-author on chapter 78. Sciomyzidae and László Papp was first author on chapter 99. Sphaeroceridae. All three were leading experts in their respective fields as the quality of their included chapters testifies.

The reader is referred to the following publications, which provide additional information on their lives and careers: Friedman, A.-L.-L. 2019. Dr Amnon Freidberg — 75 years. *Israel Journal of Entomology* **49**: i–xl.; Murphy, W.L. & Vala, J.-C. 2020. Obituary. Lloyd Vernon Knutson. *Proceedings of the Entomological Society of Washington* **122**: 251–272; Peregovits, L. & Soltész, Z. 2021. In memoriam László Papp. *Acta zoologica Academiae scientiarum hungaricae* **67**: 99–100.

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PLATYPEZIDAE 57

(Flat-footed Flies)

Peter J. Chandler

Fig. 57.1. Male of *Lindneromyia* sp. (South Africa) (photograph © S.A. Marshall).

Diagnosis

Small- to medium-sized flies (body length: 1.4–10.0 mm), humpbacked and slender to broad-bodied; secondary sexual characters apparent in most structures, sexes often differ strikingly in colouration, with males (Figs 1, 3) mainly black and females often lighter in colour (Fig. 4), variously marked, with brown, grey, silver, yellow or orange markings; females of some species also entirely dark coloured, while in others males more brightly coloured, but females usually still differ in colouration.

Head (Figs 5–7) broad; eyes large, holoptic, in contact dorsally in male (Fig. 5), but separated by more or less broad frons in female (Figs 6, 7); head setation varies, postocular and ocellar setae usually present; short frontal setae present in males of some genera (Fig. 5); strong vertical and fronto-orbital setae present in females of *Microsania* Zetterstedt and Callomyiinae (Fig. 6), these absent in Platypezinae (Fig. 7); antenna erect, with short scape and pedicel (Fig. 5); postpedicel rounded or tapered apically, with terminal 3-articled arista (Fig. 5); mouthparts short; palpus broadened apically.

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Thorax (Fig. 8) arched dorsally, with well-developed setation; acrostichal setae in single median row or absent, in latter case (Platypezinae) thorax bare between uniserial to multi-serial dorsocentral setae; postpronotal, intra-alar, notopleural, supra-alar, postalar and scutellar marginal setae variously developed; propleuron with small setae, pleura otherwise bare. Wing (Figs 9–16) broad, with subcostal vein (*Sc*) invariably reaching costal vein (*C*) and all long veins reaching margin; pterostigma may extend beyond vein R_1, with distinct margin (e.g., *Microsania* and non-Afrotropical *Melanderomyia* Kessel and *Platypezina* Wahlgren, Figs 9, 11), but in most genera represented at most by darker tinted membrane in cell *sc* (Figs 12–16); vein M_{1+2} forked (Figs 13, 14) (vein M_1 incomplete basally in *Microsania*, Figs 9, 11), or unforked (Figs 12, 15, 16); vein M_2 usually abbreviated or reduced to spur if M_{1+2} forked (Figs 13, 14); crossvein *dm–m* present (except in *Microsania*, Figs 9, 11); cell *cua* invariably present, well-developed (Figs 9, 10). Legs (Figs 18–22) short or of medium length, more or less thick, with hind tibia often broadened apically (Fig. 20), often with sexual differences in structure; hind tarsus often enlarged, especially tarsomere 1, which is longer than other tarsomeres in *Microsania* and Callomyiinae (e.g., Fig. 20), but short with tarsomere 3 usually longest in Platypezinae (Figs 21, 22), having hind tarsus more or less broad, compressed, especially in females; males of most Callomyiinae (except *Platypezina*), with fore femur bearing strong seta, sharply bent near base (termed "oxhorn seta") (Fig. 18) and hind femur with posteroventral seta near base, blunt in some non-Afrotropical *Agathomyia* Verrall (Fig. 20), but may be tapered apically (as in *Bertamyia* Kessel); females of Callomyiinae and Platypezinae with membranous areas (termed "soles") on anterior surface of hind tarsomeres 3 and 4 (Fig. 22); legs of all genera (except *Microsania*) bearing bifurcated setae (Fig. 17) mainly on medial surfaces of tibiae and tarsi.

Abdomen slender, more or less cylindrical (e.g., *Bertamyia* and *Microsania*) or broad, dorsoventrally depressed (most Platypezinae), invariably broadest at second segment; male with 6 normal abdominal segments, segments 7 and 8 reduced, twisted by circumversion (rotation through 360°); male terminalia (Figs 23, 24) reflexed beneath abdomen, usually visible externally; epandrium large, bearing articulating surstyli closely apposed or surstyli fused basally to epandrium; hypandrium extended laterally into pair of variously shaped processes (termed gonopods by Chandler 2001: 34; Chandler & Shatalkin 1998: 30); phallus short, thick (Callomyiinae), or more or less elongate and slender (*Microsania* and Platypezinae), sometimes flanked by pair of apically curved postgonites (Callomyiinae and *Microsania*) or these absent (most Platypezinae including *Lindneromyia* Kessel); female abdomen (Figs 25–27) tapered apically, with segments 7 and 8 unmodified, but short and more or less retracted into segment 6, terminating in simple ovipositor.

Among cyclorrhaphous Diptera, the Platypezidae only resemble non-Afrotropical Opetiidae, which were formerly included in the family, in having holoptic males with larger facets dorsally and the erect antenna with a terminal arista. They are distinguished from Opetiidae by the acrostichal setae, which are reduced to a single row or are absent (area between dorsocentral setae clothed in irregular setation in Opetiidae). They also differ from *Opetia* Meigen, until recently the only known extant genus of Opetiidae, by the presence of three aristomeres; there are only two in *Opetia*, but three in the recently described Chilean genus *Puyehuemyia* Amorim, Silva & Brown (Amorim *et al*. 2018), which otherwise resembles *Opetia* in its wing venation and blade-like female ovipositor. In body form, they resemble non-Afrotropical Ironomyiidae (Australasian) and Phoridae (see Chapter 59), including Sciadocerinae; families that lack male eyes with this structure and the arista is terminal in only a few Phoridae, e.g., *Conicera* Meigen. The wing venation is more complete than in Phoridae, with the subcostal vein (*Sc*) ending separately in the costal vein and vein R_1 extending to the apical half of the wing. The venation of Ironomyiidae is more similar, but these have veins M_1 and M_2 arising separately from cell *dm*, while in those Platypezidae with cell *dm* present, vein M_{1+2} forks beyond it or is unforked.

Biology and immature stages

All known larvae of this family develop in fruiting bodies of larger fungi. Chandler (2001: 69) and Rotheray *et al*. (2004) summarised present knowledge of host associations, which mainly relates to the Holarctic fauna. Most of the fungus hosts grow on wood or have mycorrhizal associations with trees and most species of the family consequently occur in forests. Those species of *Agathomyia* and *Bertamyia* that have been reared, develop internally in polypore fungi, while *Callomyia* Meigen

Figs 57.2–4. Habitus of living Platypezidae: (2) female of *Bertamyia notata* (Loew) (non-Afrotropical); (3) male of *Microsania meridionalis* Collart with phoretic mites on abdomen (non-Afrotropical); (4) female of *Lindneromyia* sp. (South Africa). Figs 2, 4 (photographs © S.A. Marshall), Fig. 3 (photograph © R. Andrade).

larvae feed externally on wood encrusting fungi (Ståhls *et al*. 2014). Some genera of Platypezinae also develop in polypore fungi, but most have larvae that feed between the gills of agarics, usually those growing on dead wood. The larval biology of *Microsania* has not been recorded, but adults are frequently found bearing clusters of phoretic mites on their abdomen (Fig. 3), which are considered likely to have originated from rotten wood or decaying vegetation.

Lindneromyia species, however, often develop in terrestrial fungi, especially the genus *Agaricus* (Agaricaceae) and may occur in grassland or other open habitats, which is presumably the case with some Afrotropical species. There are reared specimens with puparia of Afrotropical species of *Lindneromyia* and *Pamelamyia* Kessel, obtained from unidentified fungi, but these puparia have yet to be described.

The larval biology of *Microsania* is unknown, but adults of the genus are well-known as "smoke-flies", due to their strongly fumotropic behaviour, with males forming aerial swarms in the smoke of wood fires. Other genera also form aerial male swarms using gaps in the tree canopy as markers as a prelude to copulation. Both sexes may be observed rapidly running over the broad leaves of trees, shrubs or herbaceous plants in a similar fashion to Phoridae. This activity is considered to be associated with feeding on honeydew and other surface deposits on leaves, but has not been observed in the genus *Microsania*. Probably any accessible leaves may be visited by them; material examined has been recorded on leaves of Common mango, *Mangifera indica* L. (Anacardiaceae), Cassava *Manihot esculenta* Crantz (Euphorbiaceae), Banana and wild Plantain (*Musa spp.*) (Musaceae) and they have also been observed (G. Ståhls, pers. comm. 2018), on species of *Agapanthus*, *Clivia*, *Scadoxus* (all Amaryllidaceae) and on ferns.

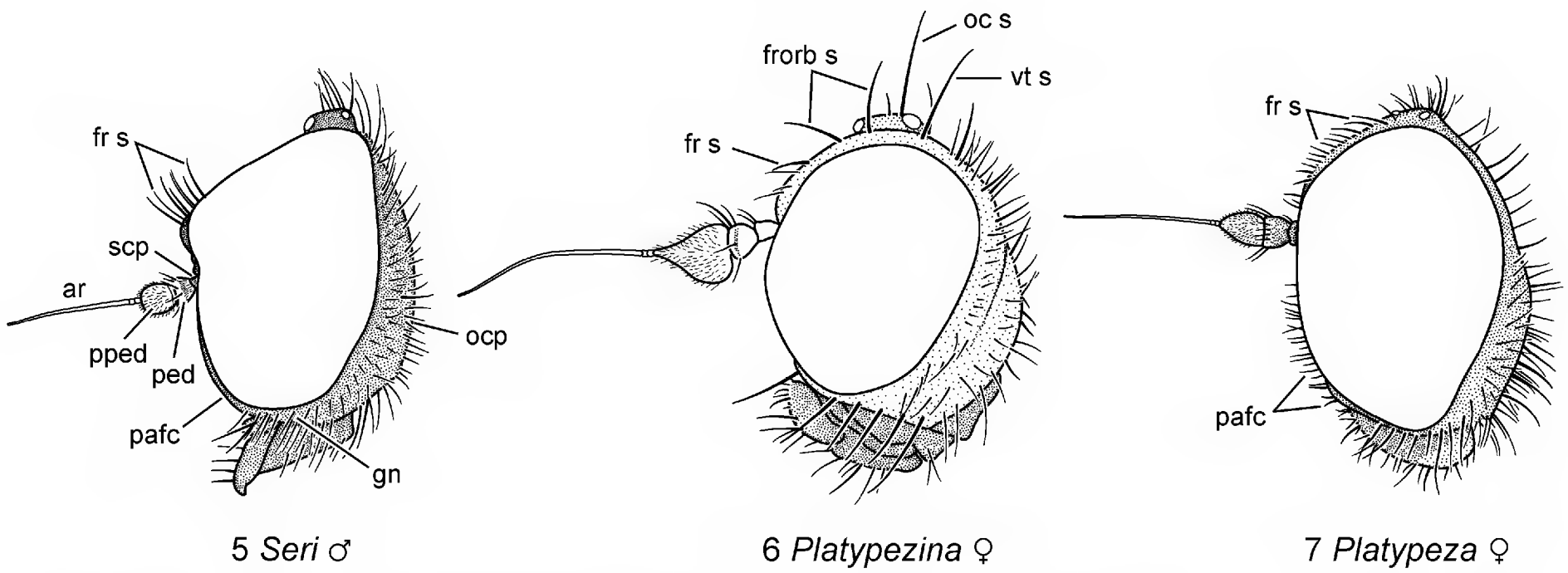
Described larvae and puparia are all of Palaearctic or Nearctic species. Chandler (2001: 75) included an identification key to the larvae or puparia of 13 genera. Rotheray *et al*. (2004) provided more detailed descriptions of the final instar larvae or puparia for 16 species in 11 genera and figured their cephaloskeletons. Larvae (Figs 28–30) are cylindrical, or more or less dorsoventrally depressed, with a small pseudocephalon bearing the short antennae and maxillary palpi (Fig. 34). The respiratory system is amphipneustic, with both prothoracic (Figs 29, 32) and posterior spiracles on short tubes (Figs 29, 33). The body usually bearing a series of short marginal and dorsal processes on each body segment (Fig. 29), of which the number and form are diagnostic for genera and species. Larvae of Callomyiinae (Fig. 28) have four pairs of processes on the last segment, while those of Platypezinae (Figs 29, 30) have at most three pairs. Puparia (Fig. 31) resemble the larvae, except the head and prothorax are fused to the ventral surface, with the mesothorax forming the anterior margin. Puparia may also be broader and more depressed than larvae.

Economic significance

No species of economic significance are currently known.

Classification

Platypezids are a small group of "primitive" cyclorrhaphous flies. Their systematic position and composition were discussed by Chandler (2001: 52), who recognised four subfamilies: Callomyiinae, Melanderomyiinae, Microsaniinae and Platypezinae; with Melanderomyiinae and Microsaniinae being monogeneric. The genus *Microsania* has a global distribution, while *Melanderomyia*, which develops in the fungal family Phallaceae, is only known from North America. Chandler (2001: 54) did not find any synapomorphy common to the entire family, and from recent research based on molecular data, Tkoč *et al*. (2016) based on a rather limited molecular dataset



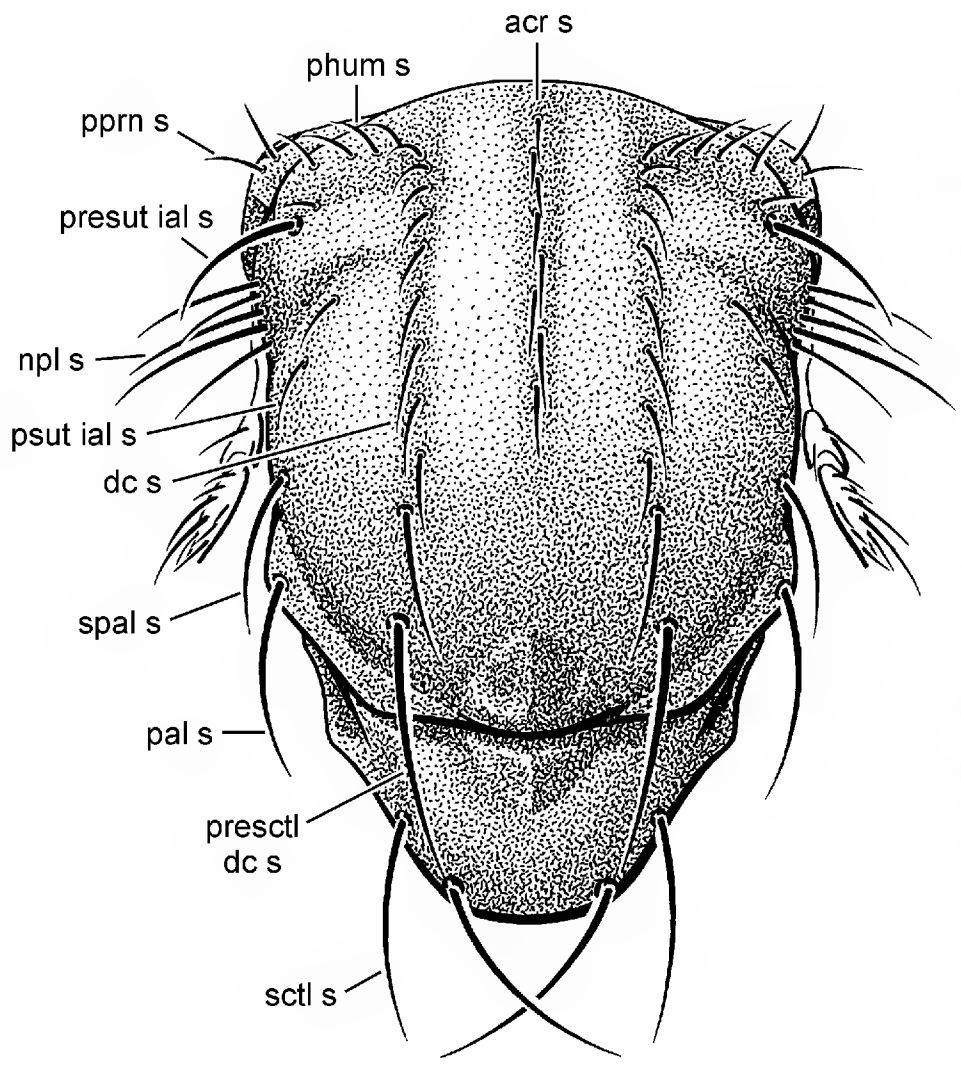
Figs 57.5–7. Heads of Platypezidae (lateral views; non-Afrotropical): (5) *Seri obscuripennis* (Oldenberg) ♂; (6) *Platypezina connexa* Boheman ♀; (7) *Platypeza fasciata* Meigen ♀. Figs 5, 6 (after Chandler & Shatalkin 1998, figs 4, 3, respectively), Fig. 7 (after Chandler 2001, fig. 30).

Abbreviations: ar – arista; fr s – frontal seta; frorb s – fronto-orbital seta; gn – gena; oc s – ocellar seta; ocp – occiput; pafc – parafacial; ped – pedicel; pped – postpedicel; scp – scape; vt s – vertical seta.

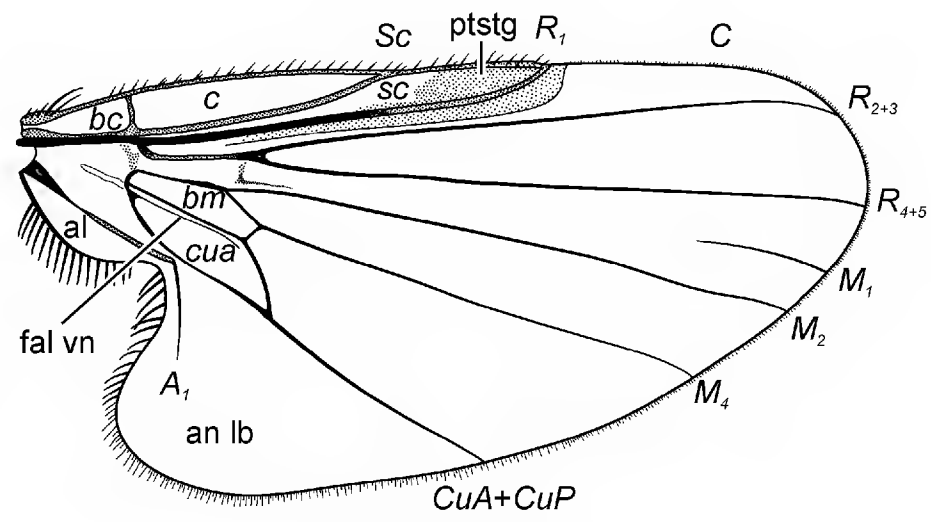
suggested that *Microsania* has a separate phylogenetic origin, while the remainder of the family is monophyletic, as are the remaining three subfamilies.

Callomyiinae includes five genera of which only one, *Bertamyia*, is recorded from the Afrotropics. The monotypic Palaearctic genus *Chydaeopeza* Shatalkin was placed in synonymy with the diverse Holarctic genus *Agathomyia* by Tkoč *et al*. (2016). They also recovered *Bertamyia* and the Holarctic genus *Callomyia* forming a clade with *Agathomyia* and concluded that *Agathomyia* is paraphyletic with respect to these other genera. Some species-groups within *Agathomyia* may need to be raised to generic rank to establish monophyletic taxa, but further work is necessary to achieve this.

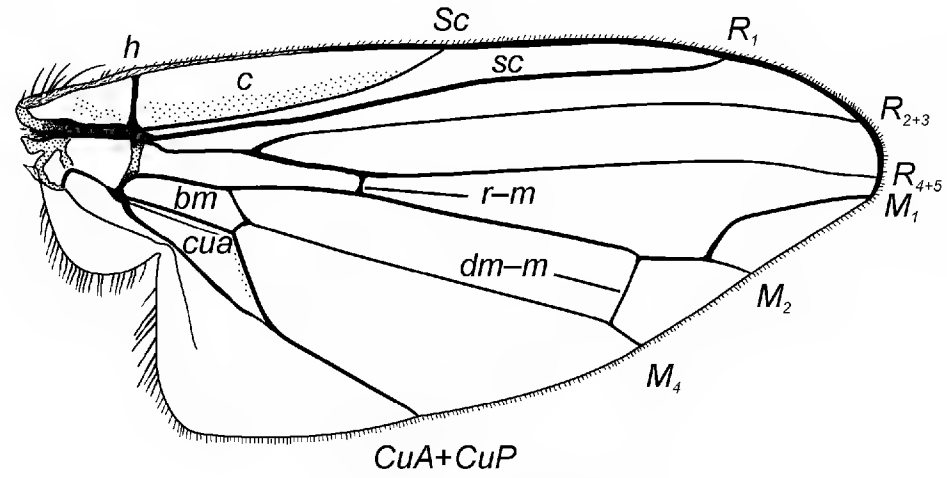
Platypezinae includes at least ten genera, of which three are known from the Afrotropics. The tropical fauna of Platypezinae is less diverse generically than that of the Holarctic Realm. The previous assignment of tropical species to genera was found to be largely incorrect in a revision of Australasian and Oriental species (Chandler 1994) and the same has proved true for Afrotropical species (Chandler, in prep.). The Neotropical fauna has not yet been critically studied, but preliminary work suggests that this is also true there (Chandler 2010: 716). Most species in these three regions belong to the large genus *Lindneromyia*, as redefined by Chandler (1994), who synonymised within it several other genera recognised by Kessel (1987: 683 and earlier works by him and his co-workers), principally based on proportional differences in wing venation. These other genera (*Grossovena* Kessel & Maggioncalda, *Penesymmetria* Kessel & Maggioncalda, *Plesioclythia* Kessel & Maggioncalda and *Symmetricella* Kessel), were found not to be tenable when other characters, such as male terminalia were studied. Some species placed in *Paraplatypeza* Kessel & Maggioncalda have also been re-assigned to *Lindneromyia* and those reported from the Afrotropics are here considered to belong



8 *Agathomyia*



9 *Microsania*



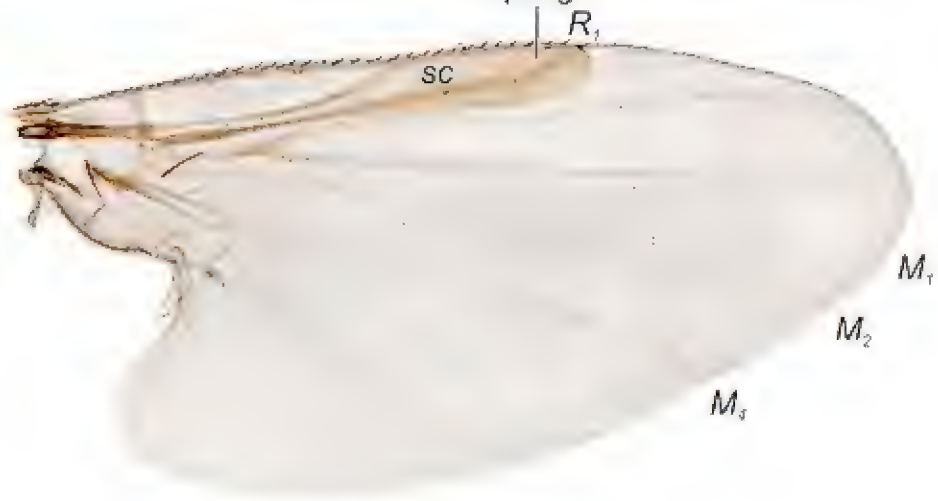
10 *Lindneromyia*

Figs 57.8–10. Thorax and wings of Platypezidae (dorsal views; non-Afrotropical): (8) thorax of *Agathomyia canadensis* Johnson; (9) wing of *Microsania pectipennis* (Meigen); (10) same, *Lindneromyia sauteri* (Oldenberg). Fig. 8 (Kessel 1987, fig. 20), Fig. 9 (after Chandler 2001, fig. 18), Fig. 10 (after Chandler 1994, fig. 43).

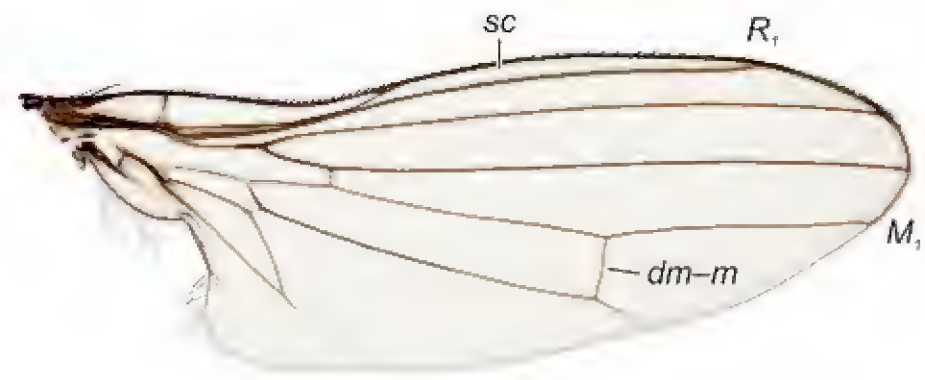
Abbreviations: A_1 – first branch of anal vein; acr s – acrostichal seta; al – alula; an lb – anal lobe; *bc* – basal costal cell; *bm* – basal medial cell; *c* – costal cell; *C* – costal vein; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; dc s – dorsocentral seta; *dm–m* – discal medial crossvein; fal vn – false vein; *h* – humeral crossvein; M_1 – first branch of media; M_2 – second branch of media; M_4 – fourth branch of media; npl s – notopleural seta; pal s – postalar seta; phum s – posthumeral seta; pprn s – postpronotal seta; presctl dc s – prescutellar dorsocentral seta; presut ial s – presutural intra-alar seta; psut ial s – postsutural intra-alar seta; ptstg – pterostigma; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *sc* – subcostal cell; *Sc* – subcostal vein; sctl s – scutellar seta; spal s – supra-alar seta.

to *Lindneromyia*. *Paraplatypeza* is currently maintained for a Holarctic group with more strongly developed chaetotaxy of the head, but *Lindneromyia* may be paraphyletic in relation to it. It has not yet been possible to define species-groups within *Lindneromyia* or to establish relationships between the regional faunas of the genus.

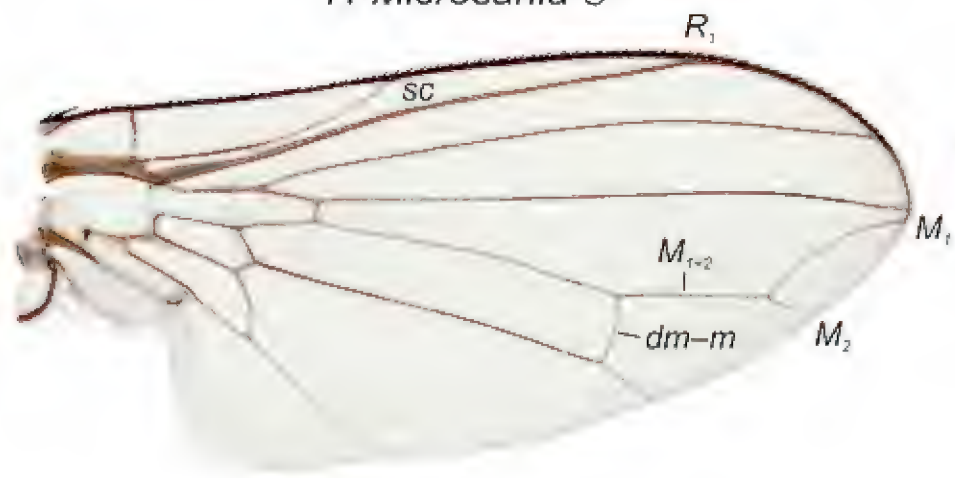
Tkoč *et al*. (2016) undertook a molecular analysis of Platypezidae, including several species of *Lindneromyia* (including four Palaearctic and three Australasian species), three species of *Paraplatypeza* (the Holarctic group as noted above) and one of *Pamelamyia*, which together were recovered as a monophyletic clade among the taxa studied. This placed *Pamelamyia* as sister-group to the remainder and *Paraplatypeza* as sister to the species included in *Lindneromyia*. For this reason *Pamelamyia* is here retained as a separate genus. It is recognised that other species of *Lindneromyia* from the Afrotropics and other regions require to be included in future phylogenetic analyses, but this has not been practicable to date, due to insufficient freshly collected material being available. This is now being remedied, however, by work in progress on generating mtDNA COI barcodes for recently collected Afrotropical specimens (G. Ståhls, pers. comm. 2018). A result of this work, is that the Afrotropical species *Platypeza thomasseti* Brunetti,



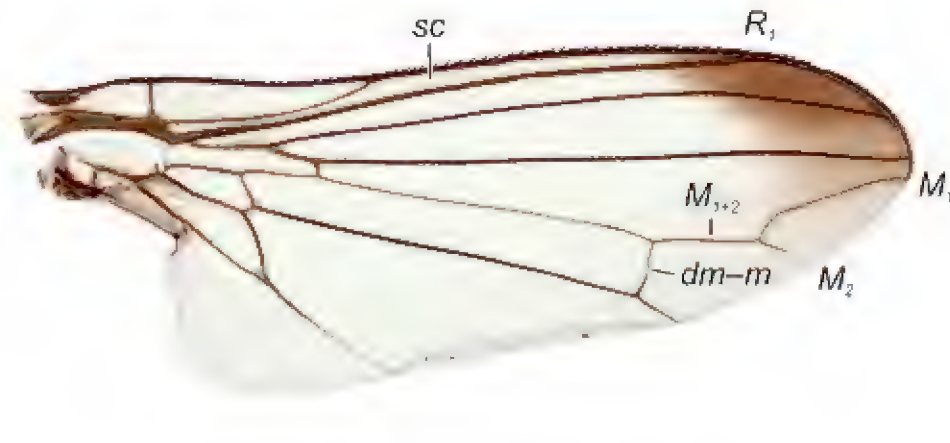
11 *Microsania* ♂



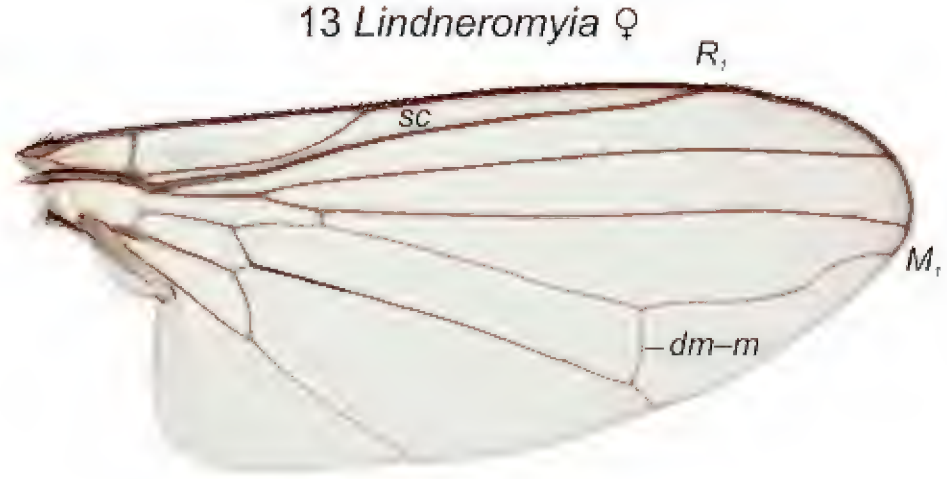
12 *Bertamyia* ♂



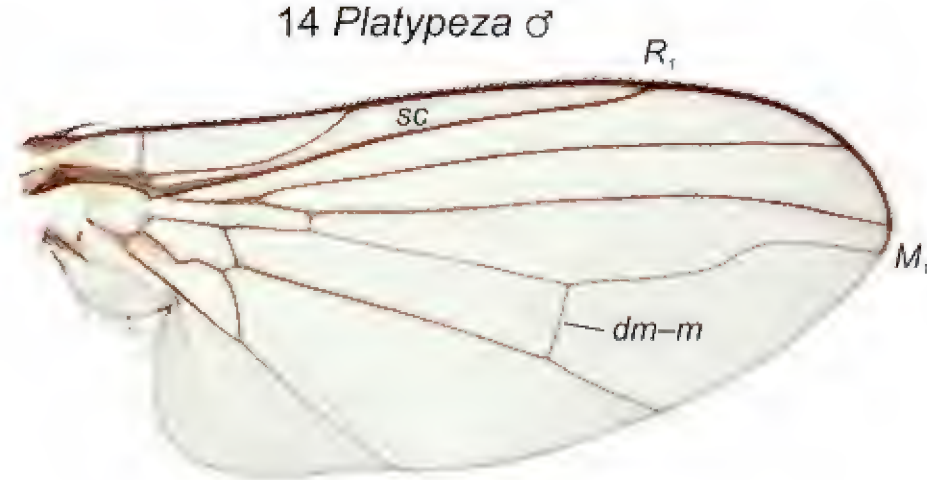
13 *Lindneromyia* ♀



14 *Platypeza* ♂



15 *Lindneromyia* ♀



16 *Pamelamyia* ♀

Figs 57.11–16. Wings of Platypezidae (dorsal views): (11) *Microsania pectipennis* Meigen ♂ (non-Afrotropical); (12) *Bertamyia umacibise* (Kessel) ♂; (13) *Lindneromyia* sp. ♀; (14) *Platypeza thomasseti* Brunetti ♂; (15) *Lindneromyia africana* Kessel ♀; (16) *Pamelamyia stuckenbergorum* Kessel & Clopton ♀.

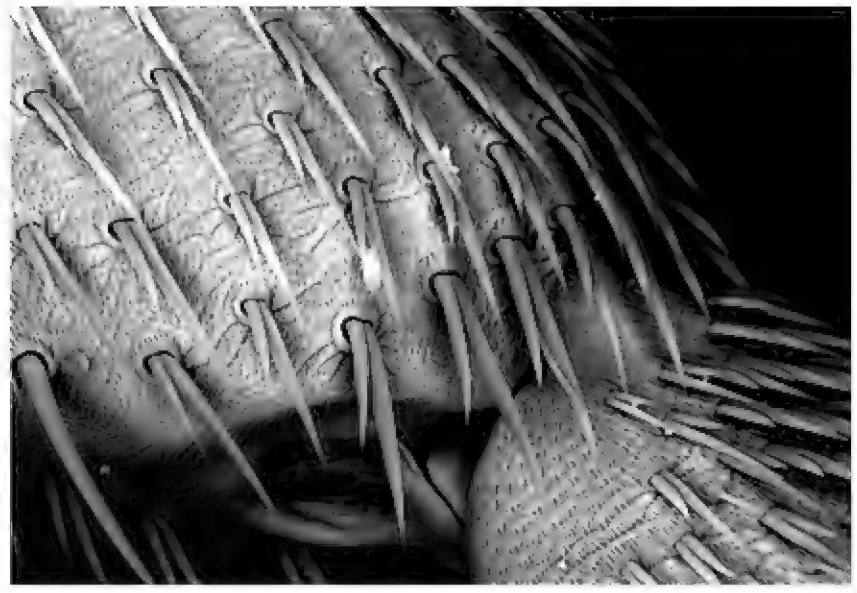
Abbreviations: *dm–m* – discal medial crossvein; M_1 – first branch of media; M_{1+2} – fused first and second branch of media; M_2 – second branch of media; M_4 – fourth branch of media; ptstg – pterostigma; R_1 – anterior branch of radius; *sc* – subcostal cell.

1929 groups with Palaearctic species of *Platypeza* Meigen. In the analysis by Tkoč *et al*. (2016) *Platypeza* was sister-group to the clade including *Lindneromyia*, *Paraplatypeza* and *Pamelamyia*. *Platypeza* is a mainly Holarctic genus, characterised by the distinctive structure of the male terminalia. As *P. thomasseti* does not share this structure and more resembles the *Lindneromyia* clade in the structure of its terminalia, it possibly represents an early branch of the *Platypeza* clade.

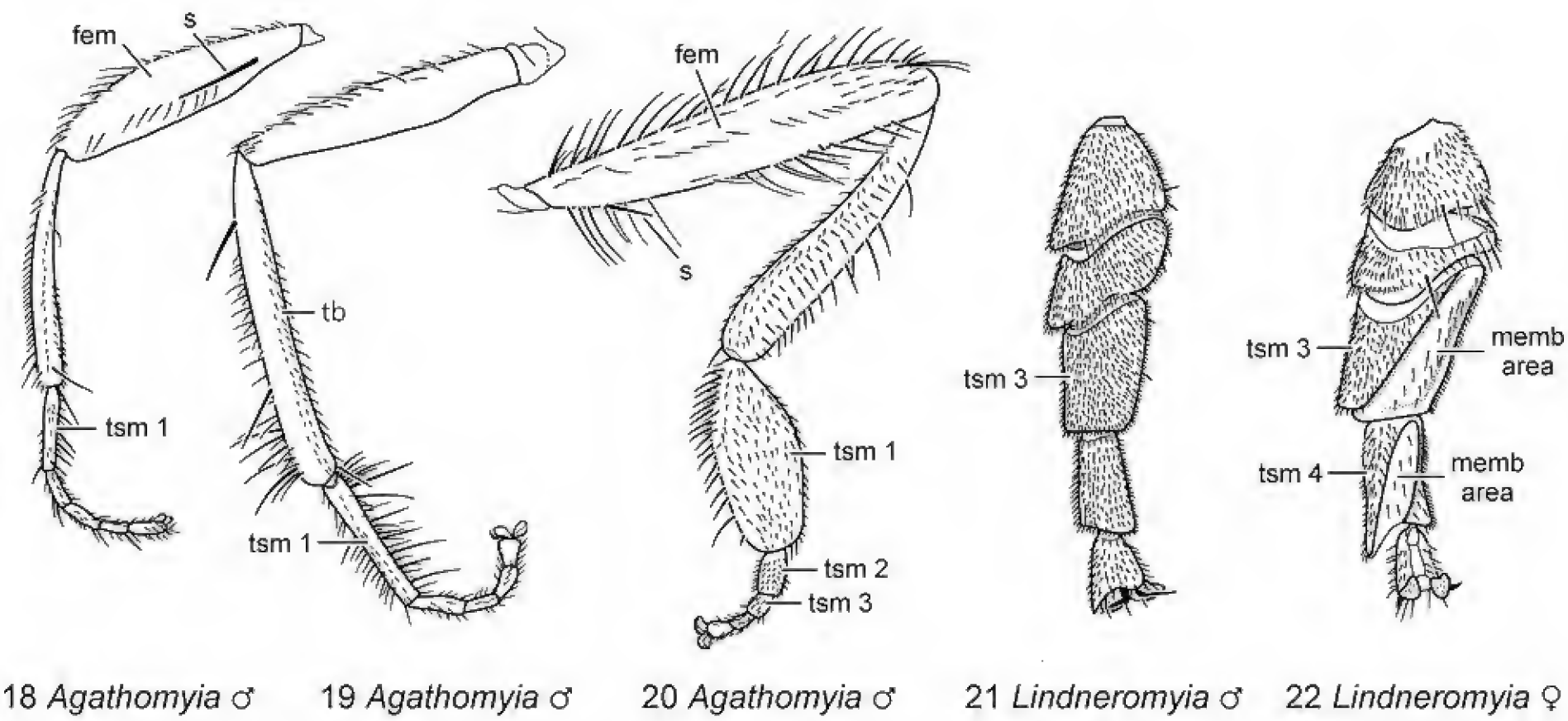
There are more than 250 described species of the family globally. In general, the number of undescribed species in collections is similar to the number of names that will be lost to synonymy and the Afrotropical fauna certainly comprises more than 40 species. Some of this confusion is due to pronounced sexual dimorphism in many species, leading to the description of the sexes under different names.

Identification

Chandler (2001: 77) provided identification keys to the four subfamilies and (2001: 98) to the three European genera of Callomyiinae and (2001: 174) eight of Platypezinae. The characters by which other genera are distinguished were also cited. Two other genera (*Chydaeopeza* (now a synonym of *Agathomyia*) and *Metaclythia* Kessel), were also included in the identification key to Palaearctic species by Chandler & Shatalkin (1998: 41). The Nearctic genera were keyed by Kessel (1987:



17 *Callomyia*



18 *Agathomyia* ♂ 19 *Agathomyia* ♂ 20 *Agathomyia* ♂ 21 *Lindneromyia* ♂ 22 *Lindneromyia* ♀

Figs 57.17–22. Legs and leg characters of Platypezidae: (17) medial surfaces of tibia and tarsus of *Callomyia amoena* Meigen (non-Afrotropical); (18) fore leg of *Agathomyia setipes* Oldenberg, posterior view ♂ (non-Afrotropical); (19) same, mid leg; (20) same, hind leg, anterior view; (21) hind tarsus of *Lindneromyia argyrogyna* (de Meijere) ♂ (non-Afrotropical); (22), same, *L. sauteri* (Oldenberg) ♀ (non-Afrotropical). Fig. 17 (after Tkoč *et al*. 2016. fig. 4), Figs 18–20 (after Chandler & Shatalkin 1998, figs 17–19), Figs 21, 22 (after Chandler 1994, figs 60, 54, respectively).

Abbreviations: fem – femur; memb area – membranous area; s – seta; tb – tibia; tsm – tarsomere.

683), who recognised the genera listed above (under "Classification"), that are now considered synonymous with *Lindneromyia*. Chandler (2010: 717) included identification keys to the seven genera known from Central and South America. Adult Platypezidae are usually preserved dry. Specimens are best micro-pinned in the field for later double-mounting (see Chapter 2). Specimens for use in molecular studies are best preserved in 80–96 % ethanol.

Key to genera of Afrotropical Platypezidae

1. Wing without *dm–m* crossvein (Figs 9, 11); vein R_1 reaching at most $^2/_3$ wing length, surrounded apically by pterostigma; vein M_{1+2} forked, but vein M_1 incomplete basally (Figs 9, 11); hind tarsomere 1 about as long as tarsomeres 2–4 in both sexes . . . . . *Microsania* Zetterstedt
– Wing with *dm–m* crossvein closing elongate cell *dm* (e.g., Figs 10, 12–16); vein R_1 longer, exceeding $^2/_3$ wing length, without pterostigma; vein M_{1+2} forked or unforked, but vein M_1 complete (e.g., Figs 10, 12–16); hind tarsomere various (as in Figs 20–22) 2
2. Thorax with acrostichal setae arranged in uniserial row (as in Fig. 8); wing vein M_{1+2} unforked (Fig. 12); hind tarsomere 1 elongate, at least as long as tarsomeres 2–4 combined (as in Fig. 20) . . . . . *Bertamyia* Kessel
– Thorax without acrostichal setae; wing vein M_{1+2} forked (e.g., Figs 13, 14) or unforked (e.g., Fig. 16); hind tarsomere 1 much shorter than tarsomeres 2–4 combined (as in Figs 21, 22) 3
3. Wing vein M_{1+2} forked (Figs 10, 13, 14) . . . . . *Lindneromyia* Kessel [in part] and *Platypeza* Meigen
– Wing vein M_{1+2} unforked or with M_2 very short (e.g., Figs 15, 16) 4
4. Length of wing crossvein *dm–m* less than length of last part of vein M_4 (Fig. 15) . . . . . *Lindneromyia* Kessel [in part]
– Length of wing crossvein *dm–m* more than length of last part of vein M_4 (Fig. 16) . . . *Pamelamyia* Kessel

Synopsis of the fauna

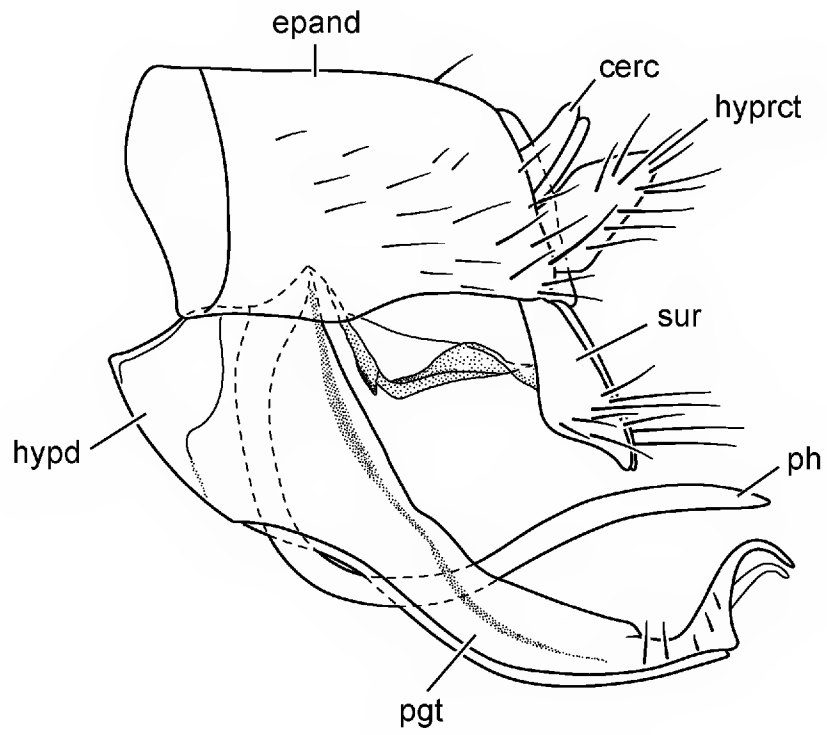
There were only scattered species descriptions in the literature, prior to Kessel & Clopton's (1970) comprehensive account of Afrotropical species, in which they re-described all the known species, treating all as valid and described 26 additional new species. The only subsequent additions were those of Bowden (1973, 1978), who described four species from Comoros and Kenya and provided the only figures then published of male terminalia for Afrotropical species. A revision of Afrotropical Platypezidae by the writer is in progress, involving examination of all surviving type material. Of 42 specific names previously proposed for Afrotropical species, only seven are based on both sexes; 18 were described from males alone and 17 from females alone. This situation has resulted from difficulty in associating the sexes, due to sexual dimorphism in structure and colouration that occurs in many species. Several synonyms have become apparent, while a comparable number of undescribed species has been recognised in examined material.

In the genus *Lindneromyia*, there are species with clearly different male terminalia that are not reliably separable on external characters alone, while some species that have external differences, e.g., in the structure of the hind tarsus, may have very similar terminalia. In some cases there is good circumstantial evidence for association of the sexes, but this is not yet possible in more than a small number of species and further description of species based only on females should be avoided. The DNA barcoding mentioned above should assist in future in the association of sexes of the same species.

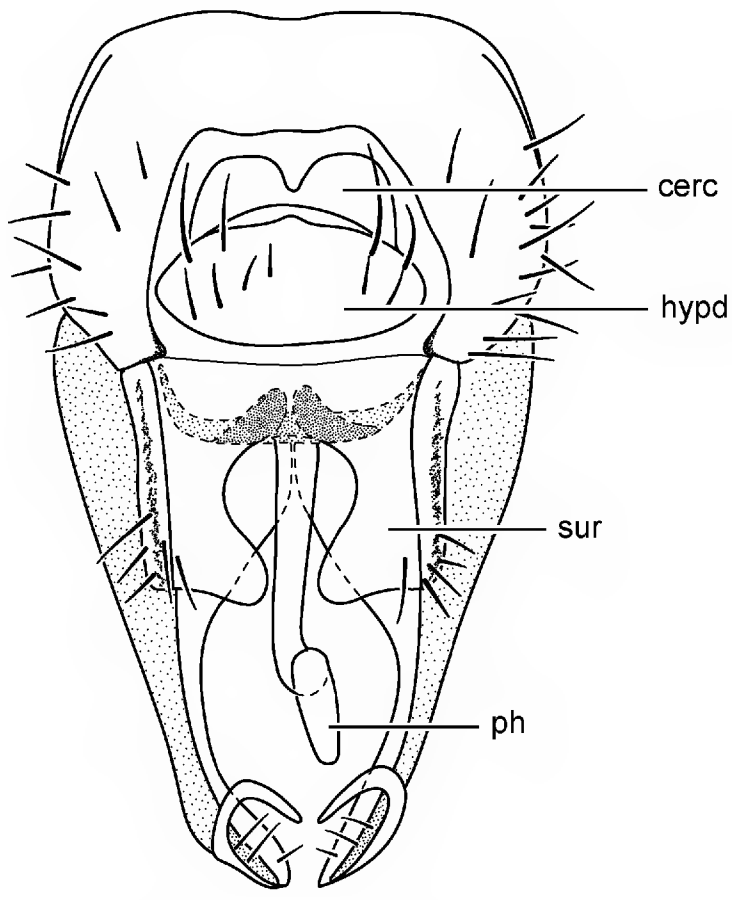
***Bertamyia* Kessel** (Callomyiinae)**.** A genus of two species occurring in the Afrotropical, Nearctic and Neotropical Regions (Fig. 2). One species, *B. umacibise* (Kessel & Clopton, 1970), occurs in the Afrotropics, recorded from South Africa and Zimbabwe. It was originally described in the genus *Agathomyia*, but was transferred to *Bertamyia* by Kessel (1970), a genus that otherwise includes only the New World species *B. notata* (Loew, 1866), recorded from Canada to Argentina. Both sexes are black, with a pattern of metallic bluish green maculae. *Agathomyia* has a postsutural supra-alar seta above the wing base in front of the postalar callus, which is absent in *Bertamyia*. The biology of *B. umacibise* remains unknown, but *B. notata* (Fig. 2) is known to develop in the soft fungus *Tyromyces* (Polyporaceae) growing on wood (Kessel 1957).

***Lindneromyia* Kessel** (Platypezinae)**.** A genus of *ca* 75 named species occurring in all zoogeographical regions, except Antarctica (Figs 1, 4). It is the dominant genus of the subfamily Platypezinae in the tropics and most described Afrotropical Platypezidae belong to the genus, which is distributed through most of the region, including Comoros, Madagascar and Afrotropical parts of the Arabian Peninsula. Of the 37 species names involved, some are synonyms, while there are at least as many undescribed species in collections. *Lindneromyia* was described by Kessel (1965) for an Afrotropical species with the median vein unforked, a character in common with *Pamelamyia*, while this vein is forked in most other species now assigned to the genus. Many of the species now referred here were described in other genera, initially in *Platypeza* (or its synonym *Clythia* Meigen), and more recently, in *Paraplatypeza*, *Plesioclythia*, *Symmetricella* and *Penesymmetria*. Most Afrotropical species placed in the aforementioned five

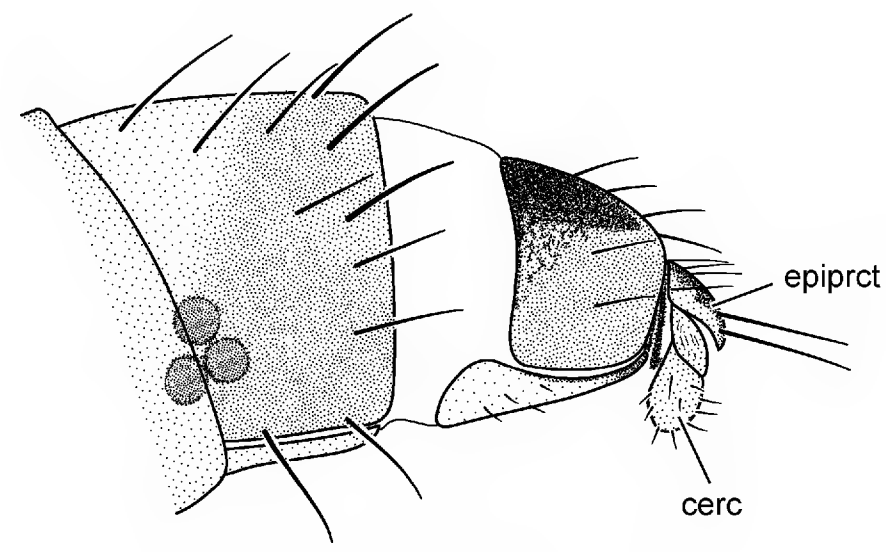
genera by Kessel & Clopton (1970) are here considered to belong to *Lindneromyia*. The males of most species have mainly dark body colouration and females may be mainly dark or have lighter grey or brown markings. One Afrotropical species, *Paraplatypeza ikekeba* Kessel & Clopton, 1970, of which only the male is known, is mainly orange-yellow in body colouration. Where the biology is known, species of the genus mainly develop in terrestrial gill fungi, especially of the genus *Agaricus*. No comprehensive identification key to Afrotropical species is currently available and the genus is in need of thorough revision.



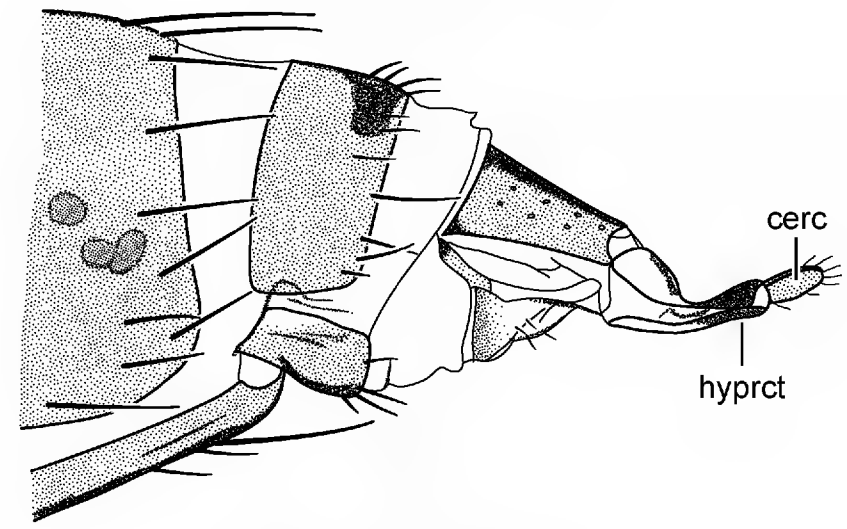
23 *Lindneromyia* ♂



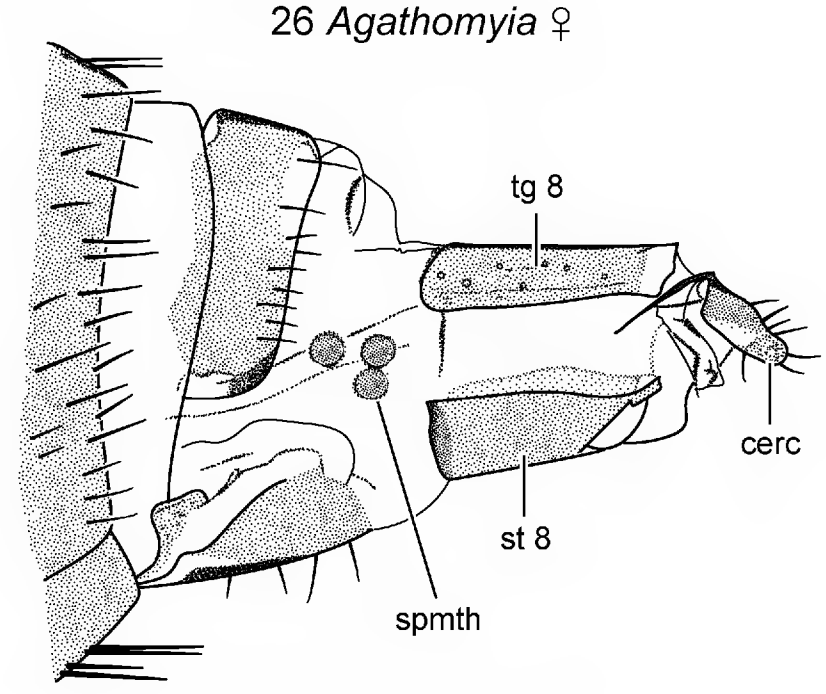
24 *Lindneromyia* ♂



25 *Microsania* ♀



26 *Agathomyia* ♀



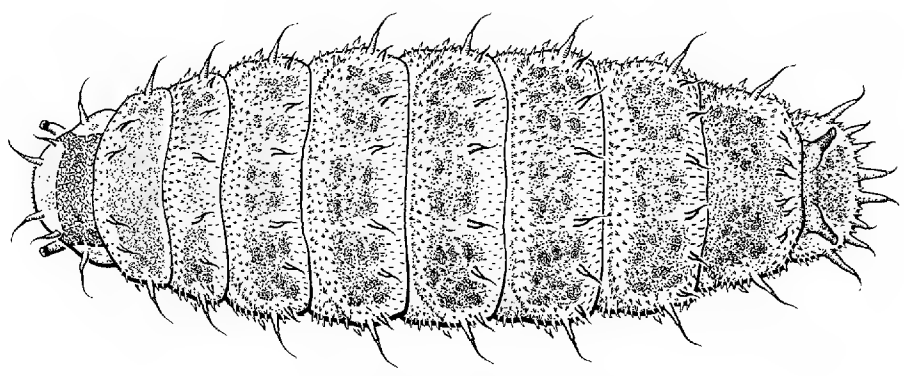
27 *Polyporivora* ♀

Figs 57.23–27. Male terminalia and female abdomens of Platypezidae (all non-Afrotropical): (23) male terminalia of *Lindneromyia argyrogyna* (de Meijere), lateral view: (24) same, posterior view; (25) female abdomen of *Microsania straeleni* Collart, lateral view; (26) same *Agathomyia antennata* (Zetterstedt); (27) same, *Polyporivora ornata* (Meigen). Figs 23, 24, 26, 27 (after Chandler & Shatalkin 1998, figs 30, 31, 34, 35), Fig. 25 (after Chandler 2001, fig. 34).

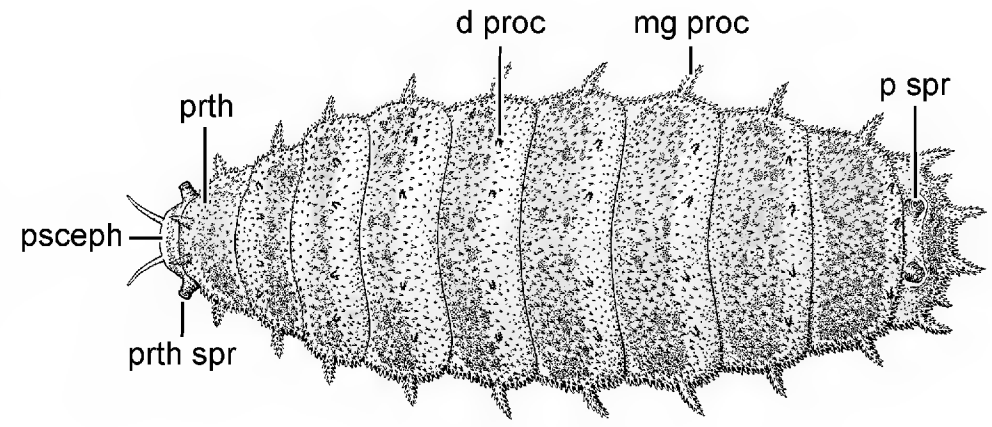
Abbreviations: cerc – cercus; epand – epandrium; epiprct – epiproct; gon – gonopod; hypd – hypandrium; hyprct – hypoproct; ph – phallus; spmth – spermatheca; st – sternite; sur – surstylus; tg – tergite.

***Microsania* Zetterstedt** (Microsaniinae)**.** A virtually cosmopolitan genus, with more than 20 species known globally (Fig. 3). It may be expected to occur widely in the Afrotropical Region, but only two species (*M. ghesquierei* Collart, 1936 and *M. alticola* Collart, 1955) have so far been described from the continental Afrotropics (Collart 1936, 1955), both from Democratic Republic of Congo. Material of an unidentified species has also been collected at a bonfire in South Africa (G. Ståhls, pers. comm. 2018). Both sexes of the genus have entirely dark body colouration. Larval biology remains unknown, but adults are usually found around smoke in which the males form aerial swarms. No identification key to Afrotropical species is currently available.

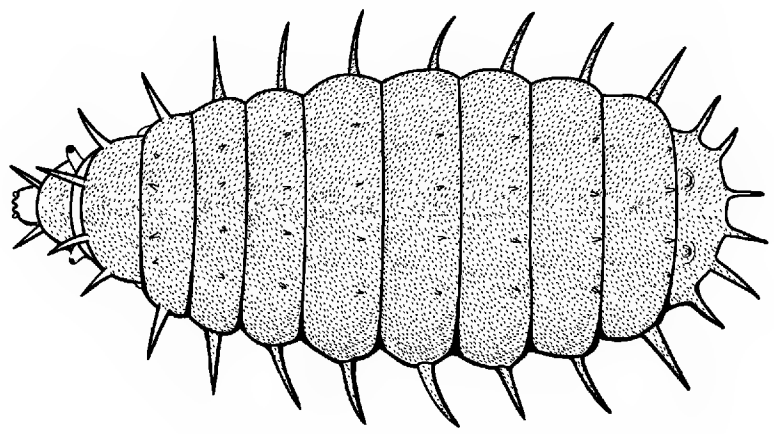
***Pamelamyia* Kessel & Clopton** (Platypezinae)**.** An endemic monotypic genus, with the single species, *P. stuckenbergorum* Kessel & Clopton, 1970, described from South Africa and subsequently recorded from Namibia and Kenya. A second undescribed species referable to the genus is known from Cameroon. Both sexes have entirely dark body colouration.



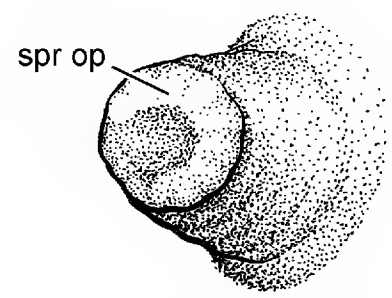
28 *Bertamyia*



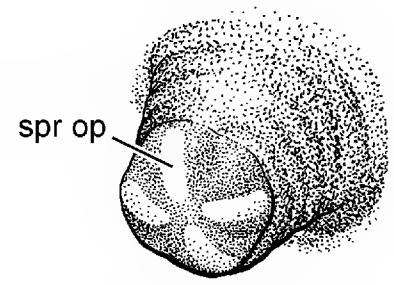
29 *Platypeza*



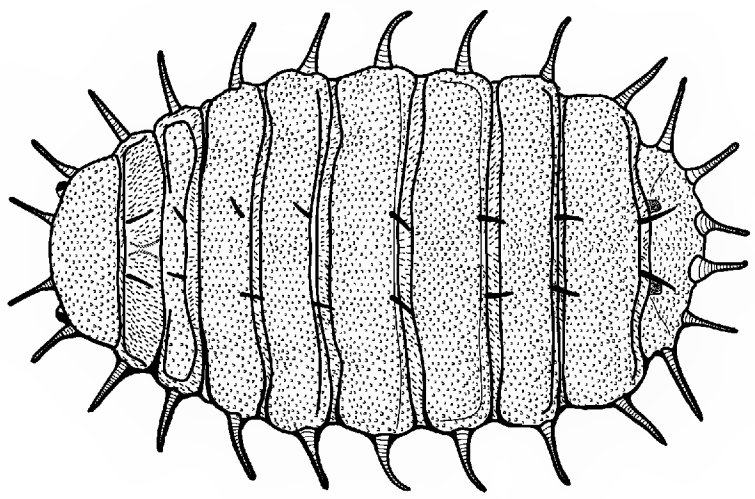
30 *Paraplatypeza*



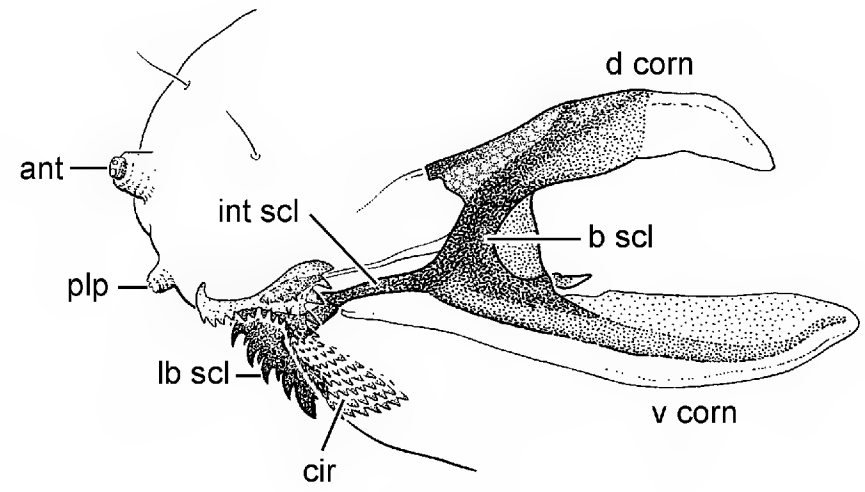
32 *Platypeza*



33 *Platypeza*



31 *Lindneromyia*



34 *Platypeza*

Figs 57.28–34. Immature stages of Platypezidae (all non-Afrotropical): (28) larval habitus of *Bertamyia notata* (Loew), dorsal view; (29) same, *Platypeza* sp.; (30) same, *Paraplatypeza atra* (Meigen); (31) puparial habitus of *Lindneromyia dorsalis* (Meigen), dorsal view; (32) prothoracic spiracle of *Platypeza* sp., posterodorsal view; (33) same, posterior spiracle, posterodorsal view; (34) pseudocephalon and cephaloskeleton of *Platypeza* sp., lateral view. Figs 28, 29, 32–34 (Kessel 1987, figs 31, 25, 26, 28, respectively), Figs 30, 31 (after Chandler & Shatalkin 1998, figs 46, 44, respectively).

Abbreviations: ant – antenna; b scl – basal sclerite; cir – cirri; d corn – dorsal cornu; d proc – dorsal process; int scl – intermediate sclerite; lab scl – labial sclerite; mg proc – marginal process; p spr – posterior spiracle; plp – palpus; prth – prothorax; prth spr – prothoracic spiracle; psceph – pseudocephalon; spr op – spiracular opening; v corn – ventral cornu.

Tkoč *et al*. (2016) confirmed that the genus belongs to a clade including *Lindneromyia* and *Paraplatypeza*. It is provisionally maintained as a distinct genus here, although the generic limits in this group require further study. Some Namibian material has been reared from a decomposing fungus, but the immature stages remain unknown.

***Platypeza* Meigen** (Platypezinae)**.** A mainly Holarctic genus, with at least 16 named species narrowly extending into the Neotropical (Costa Rica) (Chandler 2010: 719) and the Oriental Region (Myanmar) (Chandler 1994: 381). As indicated above, *P. thomasseti* (Fig. 14) has been shown by DNA barcoding to be closer to the Holarctic species of *Platypeza* than to other Afrotropical species hitherto included in *Platypeza*, that are now referable to *Lindneromyia*. It is not known if any other Afrotropical species have a similar relationship, but an undescribed Afrotropical species resembles *P. thomasseti* in having a partly brown shaded wing tip. The female of *P. thomasseti* has a shiny black frons, but this is dusted in the undescribed species with a brown wing tip, as in most other representatives of this subfamily. No structural characters that distinguish *P. thomasseti* from *Lindneromyia* have been discerned, so they are grouped together in the above identification key.

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LONCHOPTERIDAE 58

(Spear-winged Flies or Pointed-winged Flies)

Andrew E. Whittington and Ashley H. Kirk-Spriggs

Fig. 58.1. Female of *Lonchoptera* sp. (non-Afrotropical) (photograph © S.A. Marshall).

Diagnosis

Small-sized (body length: 2.0–5.0 mm), yellowish to brown flies, with strongly developed setae and distinctively pointed wing apices (Fig. 1).

Head (Figs 2–4) rounded; frons broad, with robust interfrontal, ocellar and upper fronto-orbital setae; 2 pairs of convergent inner vertical setae present, continuous with distinctive row of strongly developed postocular and subvibrissal setae (Figs 2–4); 1 pair of convergent to parallel postocellar setae; setae varying from pale to dark brown (pale colouration especially noticeable in postocular group); compound eyes dichoptic in both sexes, bare; antennal postpedicel distinctly rounded; pedicel with apical conus; antennal arista long, inserted sub-apically, with 2 basal articles (Fig. 2).

Thorax (Fig. 1) elongate, dorsally convex; setae comprising 2 notopleural setae, 1 or 2 anepisternal setae, single pairs of diminutive presutural dorsocentral, presutural intra-alar, postsutural intra-alar, postpronotal, supra-alar, postalar and apical scutellar setae and weak prescutellar dorsocentral setae, plus 3 strong dorsocentral setae. Scutellum triangular, slightly wider than long. Wing (Figs 5, 6) with membrane hyaline or tinged, with sexually dimorphic venation, pointed at apex; crossveins only situated at wing base; basicosta usually with pair of strong setae; longitudinal veins bearing dark dorsal setae; vein R_1 short, bearing short dark setae; veins R_{2+3} and R_{4+5} converge apically; veins M_1 and M_2 present; vein *CuA+CuP* reaching hind margin in male (Fig. 5), but ending in vein M_4 in female (Fig. 6), thereby producing combined vein M_4+*CuA+CuP* leading from junction of vein *CuA+CuP* with vein M_4 to posterior wing margin. Legs (Fig. 1) moderately slender, femora

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2021. Manual of Afrotropical Diptera. Volume 3. Brachycera—Cyclorrhapha, excluding Calyptratae. *Suricata* 8. South African National Biodiversity Institute, Pretoria; pp. 1375–1381.

and tibiae with strong setae situated in species-specific positions (Whittington 1991).

Abdomen usually with tergites 1 and 2 fused (distinct suture visible between two tergites in some specimens), followed by 5 visible tergites; ventrally 1 + 2 and 5 sternites; male terminalia (Figs 7, 8) folded beneath abdomen; epandrium variable in size; cercus short, setulose; hypandrium U-shaped, often fused with other terminalia structures; postgonites often with additional lobes and distinctive setae; phallus with complex basal structures (Hennig 1976; Stuckenberg 1963); subepandrial sclerite usually well-developed, with setae or spines; female terminalia (Fig. 9) with cercus small to moderate in size; hypoproct small, but distinct, setulose to barely discernible; 2 ducted spermathecae present, but weakly sclerotised; tergite and sternite 9 absent in all species (Klymko & Marshall 2008) and sclerites labelled as such in Peterson (1987) and Stuckenberg (1963) need to be carefully re-evaluated.

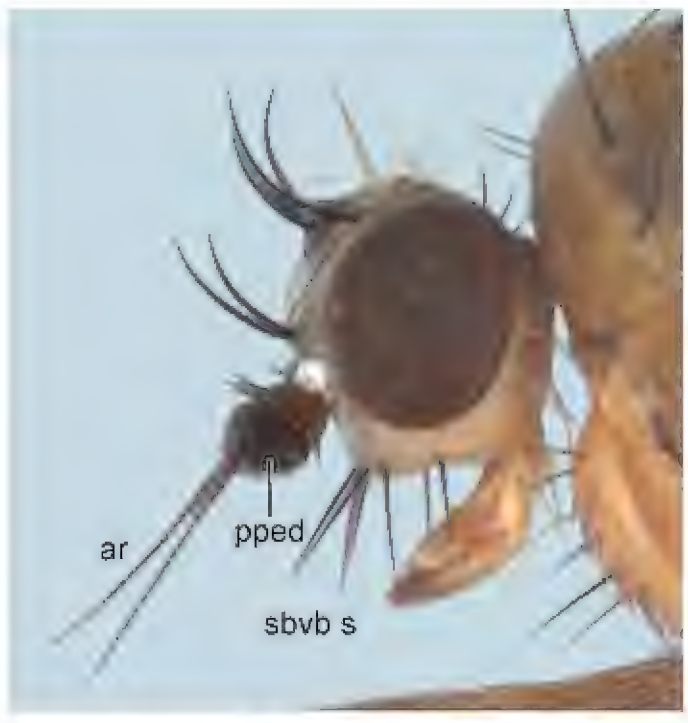
Lonchopteridae are unlikely to be confused with other families of Diptera, as a consequence of their distinctively pointed wings. The only other family with pointed wings is the Psychodidae (see Chapter 24), which is readily distinguished by the multi-segmented filamentous antennae and some brachypterous Phoridae (see Chapter 59), which lack the complex wing venation apparent in Lonchopteridae.

Biology and immature stages

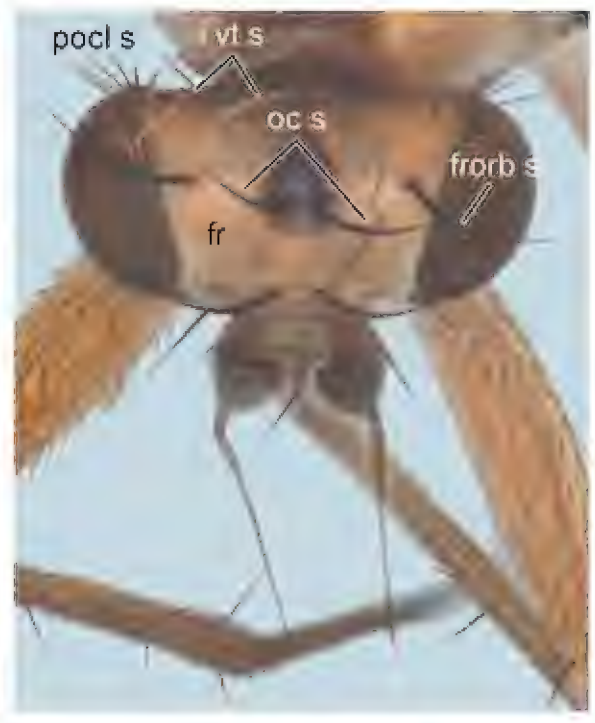
Adults feed on fungi, nectar, pollen and dead insects (Klymko & Marshall 2008) and most display eurytrophic habitat selection, ranging from deciduous forests to dry meadows (Andersson 1970; Bährmann & Bellstedt 1988), to dry leaf litter in humid environments, where larvae scrape micro-organisms from fallen leaf surfaces (Ferrar 1987: 213), to woodland (Chandler 2017; Drake 1996) and commonly occur in damp/wet situations, such as margins of streams and pools, wetlands and fens (Drake 2002) and upland peatlands (Holmes *et al*. 1991). Drake (2002), for example, lists a large array of vegetation types that Lonchopteridae are associated with in Great Britain.

Less is known regarding the biology of *Lonchoptera* Meigen, 1803 in the Afrotropical Region. Stuckenberg (1963) noted that both *L. transvaalensis* Stuckenberg, 1963 and *L. vesperis* Stuckenberg, 1963 are associated with montane grassland at elevations of > 1,750 m, with comparatively high rainfall (± 1,500 mm per annum), with adults becoming more active in the evenings. Likewise, *L. acinaris* (Séguy, 1938) is known from Mt Kenya at elevations of 853–975 m and Mt Elgon at an elevation of 1,067 m, while the only two known specimens of *L. ugandensis* Whittington, 1991, were described from the Ruwenzori Range, at an elevation of 2,530 m and Mt Sabyinyo at 2,438 m, although no habitat information is provided on the specimen labels. Specimens of *L. rava* Whittington, 1991 were collected from house lights, a mercury-vapour light trap, or swept during daytime from densely shaded streamside vegetation (± 1,000 m) and in open sunlight at sewage maturation ponds (1 specimen; ± 650 m). *Lonchoptera transvaalensis* and *L. vesperis* are both associated with fast-flowing clear streams, whereas *L. rava* was sampled along a sluggish, slow-moving, shallow stream in dense shade.

The large female to male ratio in *L. bifurcata* (Fallén, 1810) suggests that parthenogenesis occurs in this species (Stalker 1956). Collin (1938) proposed that the rareness of males may be due to their nocturnal habits, leading to preferential collecting, although Andersson (1970) sampled males during daylight hours. There is clearly a skewed sex ratio in *L. bifurcata* and



2 *Lonchoptera*



3 *Lonchoptera*

4 *Lonchoptera*

Figs 58.2–4. Heads of Lonchopteridae: (2) *Lonchoptera bifurcata* (Fallén), lateral view; (3) same, dorsal view; (4) same, frontal view. Figs 2–4 (© Trustees of Natural History Museum, London).

Abbreviations: ar – arista; fr – frons; frorb s – fronto-orbital seta; infr s – interfrontal setae; i vt s – inner vertical setae; oc s – ocellar setae; pocl s – postocular seta; pped – postpedicel; sbvb s – subvibrissal setae.

this thelytokous species displays both diploidy and triploidy (Gokhman & Kuznetsova 2018) – thelytoky is a type of parthenogenesis in which females are produced from unfertilised eggs.

In a survey conducted in northern England, Coulson & Butterfield (1982) noted that almost 39% of *L. lutea* (Panzer, 1809) and 14% of *L. bifurcata* (as *L. furcata* (Fallén, 1823)) were males, whereas Bährmann & Bellstedt (1988) recorded 3,641 specimens from Thuringia, Germany, all of which were female. Andersson (1970) encountered a bisexual population of *L. bifurcata* in Bjarnarey, Iceland during daytime and Klymko & Marshall (2008) examined 2,500 female Nearctic specimens but found no males in collections. In the Afrotropical Region, Kassebeer (2002) collected 44 specimens (all females) from Réunion Is. and on a separate occasion, the junior author collected 76 specimens from Réunion Is. all female. In addition, the 24 specimens of *L. bifurcata* from the continental Afrotropics, examined in preparation of this chapter, were all females. As Stalker (1956) pointed out, the absence (or infrequence) of males in a particular species is not proof of parthenogenesis. Stalker (1956) concluded that parthenogenesis in Nearctic *L. bifurcata* is possibly of recent origin, as European populations comprised males and by the fact that only *ca* 90% of eggs develop, resulting in imperfect parthenogenesis. Further, facultative parthenogenesis is susceptible to improvement under selection (Stalker 1954), as infrequent, but successful development of unfertilised eggs to form fertile diploid females may result in a gradual increase in the rate of parthenogenesis over numerous generations. Sampling of Afrotropical *L. rava* indicated that parthenogenesis could occur in other species of the genus (A.E. Whittington, pers. obs.). A mixed collecting protocol (house lights, mercury-vapour light trapping and daytime sweeping) revealed only one male among the 25 female specimens sampled.

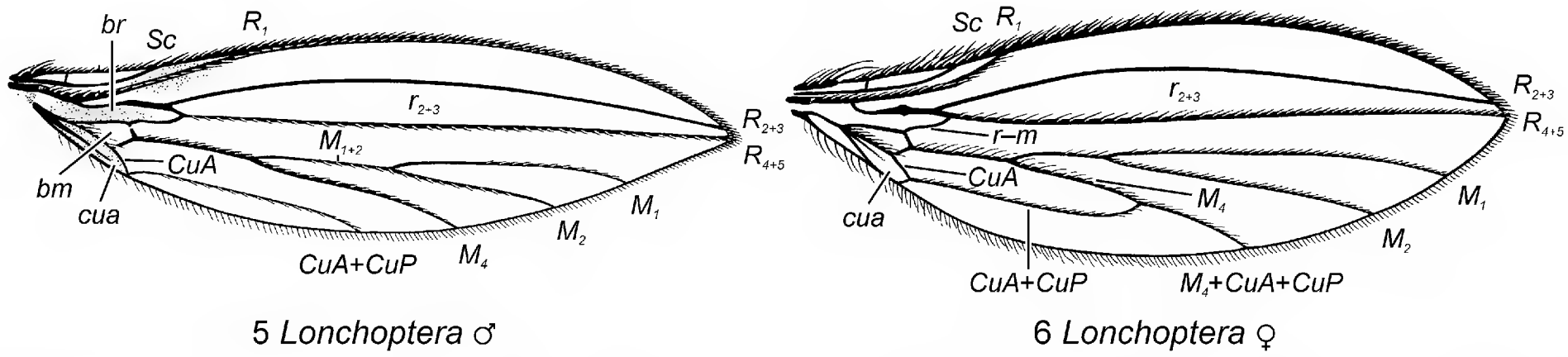
The egg of *L. bifurcata* and *L. lutea* were described by de Meijere (1906) as white, broadly oval, 0.6 mm long by 0.25 mm broad, slightly flattened on one side and slightly more pointed at one end, with no sculpture on the chorion. There are thought to be numerous larval instars: > 3 (Ferrar 1987: 213) or 6 (Baud 1973). Larvae are saprophagous, microphagous or presumably mycetophagous (Barták 1998: 15) scavengers, feeding on rotting vegetative matter, perhaps including mushrooms, bracket fungi and fungal spores (Jones 1976*a*, *b*), or wet or semi-aquatic environments, under small rocks on shingle shorelines (Chandler 2017; Drake 1996) and at springs and seeps (Vaillant 2002).

Larval stages were described by Baud (1973), de Meijere (1900, 1906); Drake (1996), Lundbeck (1916: 594); Nielsen *et al*. (1954); Peterson (1987: 675) and Smith (1969). Larvae are somewhat fusiform and dorsoventrally flattened, late instar mature larvae are 4 mm long by 2 mm broad (Ferrar 1987: 213), narrow anteriorly and blunt posteriorly; the head bears filiform antennae and mouthhooks are evident (Fig. 10). Ferrar (1987: 214) and Rotheray & Gilbert (2008), reported a cephaloskeleton that is primitive compared to other cyclorrhaphous families (Figs 11, 12): dorsal and ventral cornua are present, with an extensive area of cibarial ridges. The thorax (Fig. 10) has two pairs of long bristle-like processes and the abdomen is seven-segmented (poorly defined ventrally), each tergite plate-like, with a short lateral margin overlapping the sides of the body. The last segment has one pair of long backwardly directed marginal processes. Larvae have an amphipneustic respiratory system (Barták 1998: 15; Smith 1969), with only the first and last pair of spiracles functional and set on stalk-like processes (Ferrar 1987: 214).

The puparium resembles the larva, as pupariation occurs inside the hardened skin of the final free-living larval stage (Ferrar 1987: 214). The cuticle darkens to dark brown with age; there is a pair of short pupal respiratory horns almost indiscernible emerging through two clear maculae previously visible dorsally on abdominal segment 2 of the last larval instar (Ferrar 1987: 214). A T-shaped dorsal dehiscence permits adult eclosion from the puparium (Ferrar 1987, fig. 45.15).

Economic significance

No species of Lonchopteridae are known to be of economic significance. In Europe, *L. lutea* can be common in agricultural



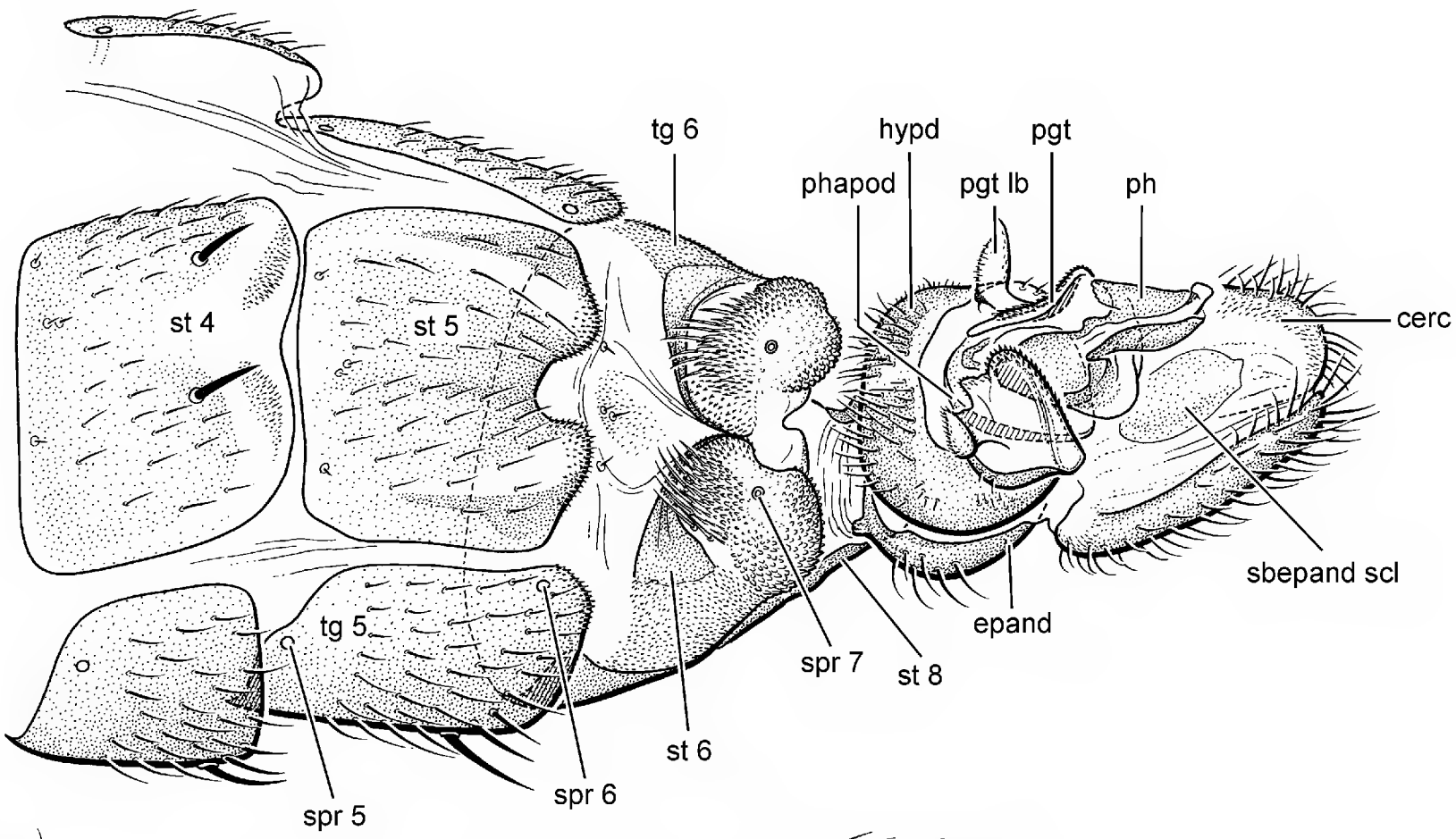
Figs 58.5–6. Wings of Lonchopteridae (dorsal views): (5) *Lonchoptera uniseta* Curran ♂ (non-Afrotropical); (6) same, *L. bifurcata* (Fallén) ♀. Figs 5, 6 (Peterson 1987, figs 3, 2 (as *furcata*), respectively).

Abbreviations: *bm* – basal medial cell; *br* – basal radial cell; *CuA* – anterior branch of cubital vein; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; M_1 – first branch of media; M_{1+2} – fused first and second branch of media; M_2 – second branch of media; M_4 – fourth branch of media; M_4+*CuA*+*CuP* – fourth branch of media + anterior branch of cubital vein + posterior branch of cubital vein; R_1 – anterior branch of radius; r_{2+3} – second + third radial cell; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Sc* – subcostal vein.

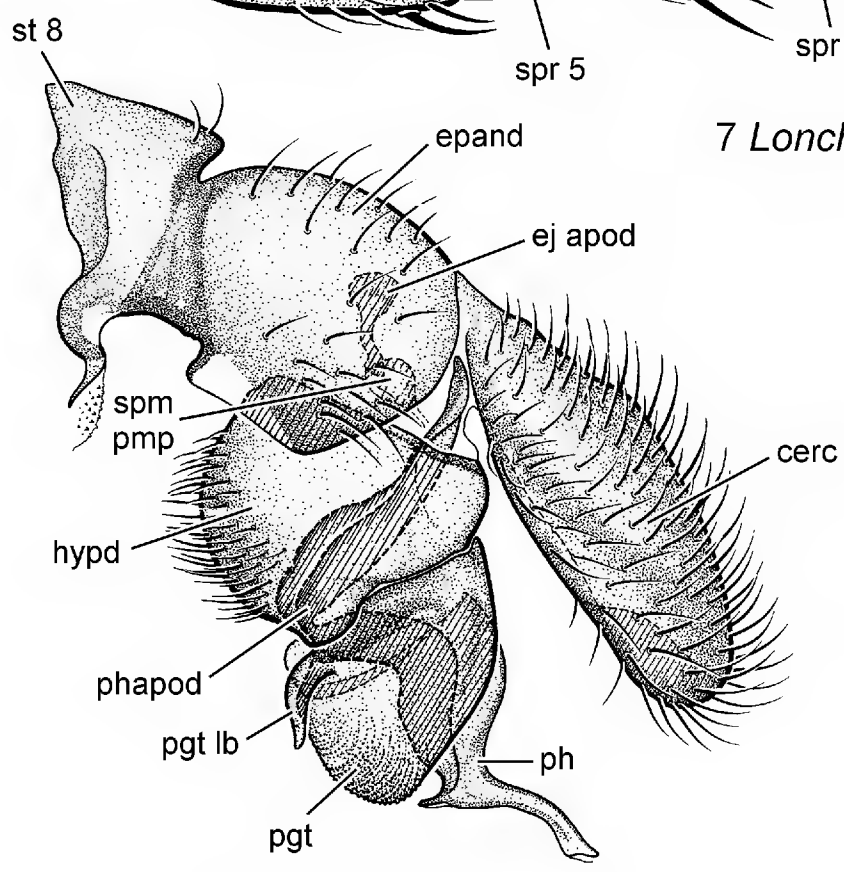
fields (Jones 1976*a*) and stubble (Jones 1972, 1973, 1976*b*). More importantly, this species was reported as representing 19–62% of the dipterous fauna in cereal crops in south-east England (Jones 1979; Potts & Vickerman 1974), although the occurrence of this species in these locations may be as a detritivore, rather than as a pest. Andersson (1991) noted that the parthenogenetic form of *L. bifurcata* was widely dispersed by human activities, hence it is often referred to as synanthropic.

Classification

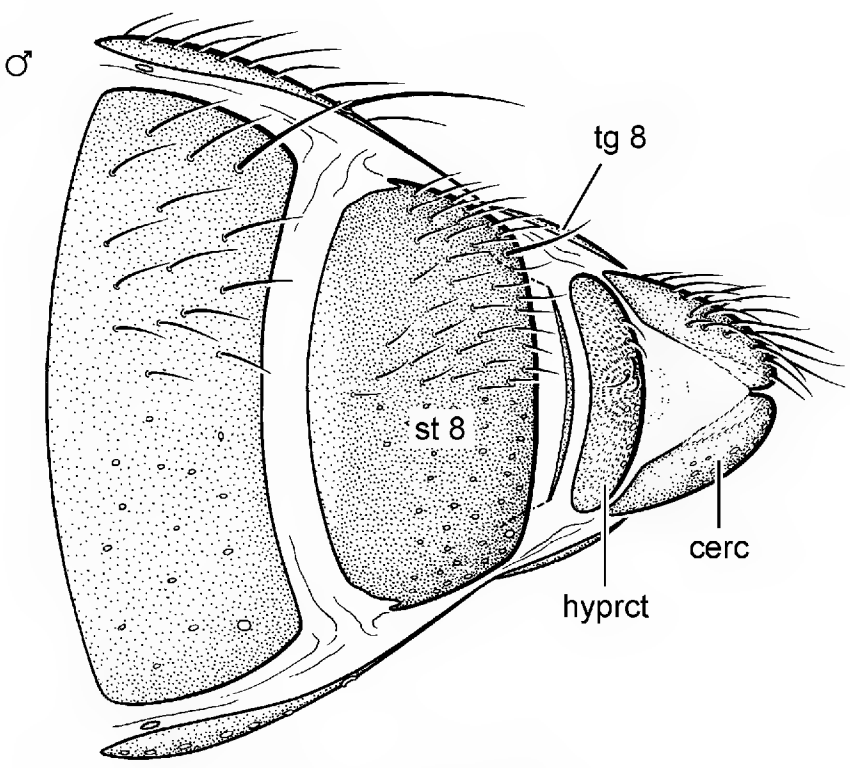
The phylogenetic relationship of the Lonchopteridae within the Cyclorrhapha has undergone a transitional history, with earlier authors sometimes placing the family within orthorrhaphous Brachycera and at other times, in the cyclorrhaphous Brachycera. Griffiths (1972: 314) placed Lonchopteridae as the only family in the subphalanx Acroptera (within the



7 *Lonchoptera* ♂



8 *Lonchoptera* ♂



9 *Lonchoptera* ♀

Figs 58.7–9. Male and female terminalia of Lonchopteridae: (7) male terminalia of *Lonchoptera uniseta* Curran, ventrolateral view (non-Afrotropical); (8) same, left lateral view; (9) female abdomen of *L. bifurcata* (Fallén). Figs 7–9 (Peterson 1987, figs 6, 5, 4 (as *furcata*), respectively).

Abbreviations: cerc – cercus; ej apod – ejaculatory apodeme; epand – epandrium; hypd – hypandrium; hyprct – hypoproct; pgt – postgonite; pgt lb – postgonite lobe; ph – phallus; phapod – phallapodeme; sbepand scl – subepandrial sclerite; spm pmp – sperm-pump; spr – spiracle; st – sternite; tg – tergite.

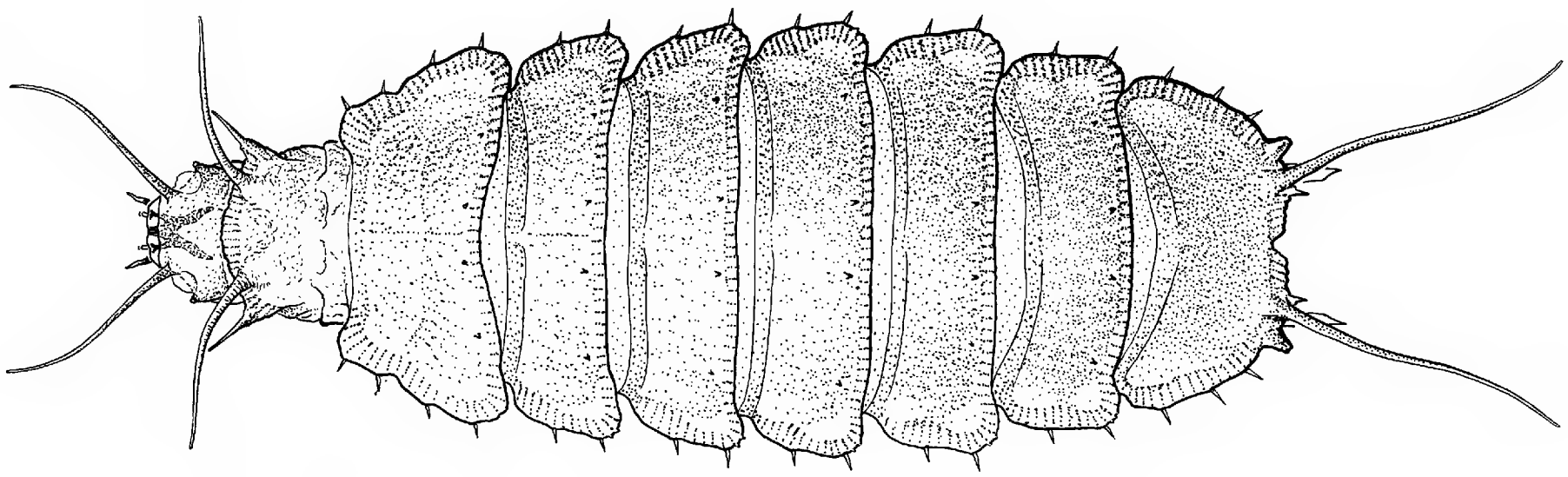
phalanx Cyclorrhapha), the remainder of the Cyclorrhapha being assigned to the subphalanx Atriata. Hennig (1976) refuted the sister-group argument for Lonchopteridae and the rest of the Cyclorrhapha. Subsequently, Peterson (1987: 679) and McAlpine (1989: 1422), rather than placing the family in a superfamily of its own, positioned Lonchopteridae as a highly specialised representative of the Platypezoidea, defined by the shared synapomorphic loss of the holoptic condition in males in Lonchopteridae and Phoridae and non-Afrotropical Ironomyiidae and Sciadoceridae. The most obvious autapomorphic character of the Lonchopteridae is the peculiar, pointed wings (McAlpine 1989: 1422).

More recently, Cumming *et al*. (1995) posited Lonchopteridae as an early branching group within the Cyclorrhapha, placed with the non-Afrotropical Ironomyiidae and Opetiidae and the Phoridae and Platypezidae, with possible sister-group affiliations to the Opetiidae (Collins & Wiegmann 2002). The most complete phylogeny of Diptera to date (Wiegmann *et al*. 2011), placed the Lonchopteridae as the most early branching group within the Platypezoidea.

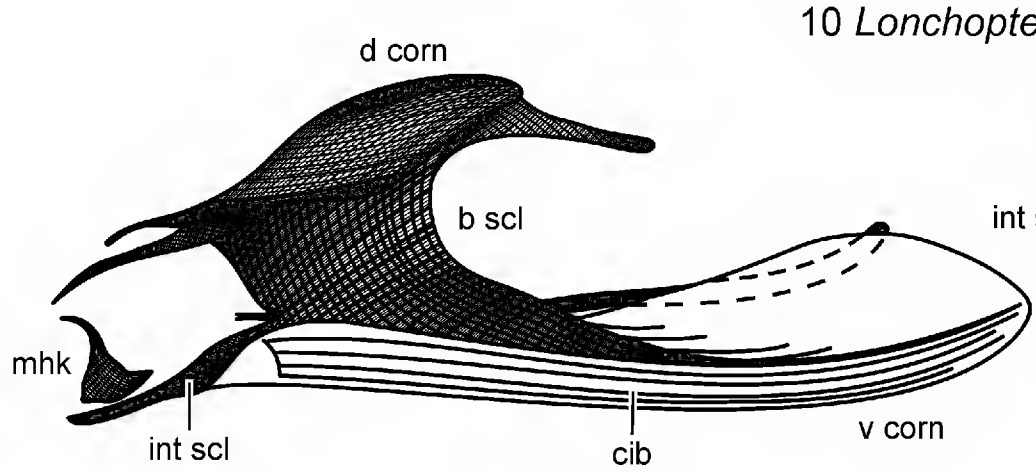
The extant family is dominated by the genus *Lonchoptera* which is represented by 65 extant species (Whittington, unpubl.). Various authors have suggested splitting the family into a greater number of genera, although none of these have gained full support (Barták 1998: 13; Klymko & Marshall 2008; Sinclair & Cumming 2006). Irrespective, only *Lonchoptera* occurs in the Afrotropical Region, where seven species are currently known.

In older literature the name *Musidora* Meigen, 1800 is frequently, but incorrectly, applied as a valid generic name for *Lonchoptera*. The publication by Meigen (1800) was suppressed by ICZN (1963) opinion 678 and the valid accepted generic name is *Lonchoptera*, as discussed by Evenhuis & Pape (2017). The genus *Dipsa* Fallén, 1810 was moved out of synonymy by Vaillant (1989) on the basis of a single putative synapomorphy (the desclerotisation of the subepandrial sclerite), which was not supported by the phylogenetic analysis of Nearctic species (Klymko & Marshall 2008). In agreement with Chandler (1998) and Klymko & Marshall (2008), the status of *Dipsa* Fallén, 1810 is accepted here as a junior synonym of *Lonchoptera*.

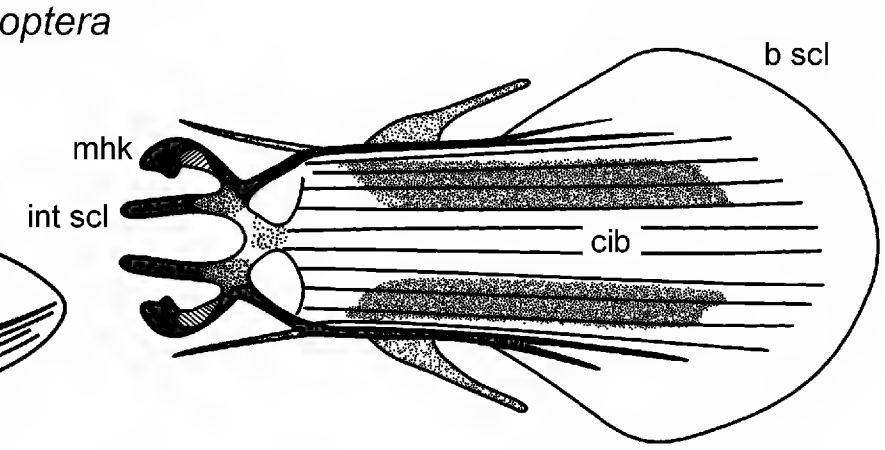
Two fossil genera, *Lonchopterites* Grimaldi & Cumming and *Lonchopteromorpha* Grimaldi & Cumming were described from Lebanese Amber (Grimaldi & Cumming 1999), although the authors questioned their familial placement. Based on wing venation and shape, these specimens may be closer to non-Afrotropical Opetiidae than to Lonchopteridae.



10 *Lonchoptera*



11 *Lonchoptera*



12 *Lonchoptera*

Figs 58.10–12. Immature stages of Lonchopteridae: (10) larval habitus of *Lonchoptera* sp., dorsal view (non-Afrotropical); (11) larval cephaloskeleton of *Lonchoptera* sp., lateral view (non-Afrotropical); (12) same, ventral view. Fig. 10 (Peterson 1987, fig. 7), Figs 11, 12 (after Hennig 1952, figs 85, 86).

Abbreviations: b scl – basal sclerite; cib – cibarium; d corn – dorsal cornu; int scl – intermediate sclerite; mhk – mouthhook; v corn – ventral cornu.

Identification

Specimens of Afrotropical *Lonchoptera* are not readily encountered, although perhaps overlooked in field conditions and are represented in museum collections by rather few specimens. The family diagnosis also serves to clearly identify *Lonchoptera*, which is the only genus that occurs in the Afrotropical Region. Specimens are best micro-pinned in the field for later double-mounting (see Chapter 2). Identification of species is usually based on tibial setation, characters of wing venation and male and female terminalia (Stuckenberg 1963; Whittington 1991).

Synopsis of the fauna

***Lonchoptera* Meigen**. A genus of 65 described species occurring in all zoogeographical regions, except Antarctica, with seven species now recorded from the Afrotropics (Whittington 1991). The first described Afrotropical species was *L. africana* Adams, 1905, based on a single female specimen from near Harare, Zimbabwe (not Kenya, as erroneously stated by Whittington 1991); this species is now known to extend to KwaZulu-Natal Province, South Africa (Whittington, unpubl.). Malloch (1932) reported the widely distributed *L. furcata*, now recognised as a junior synonym of *L. bifurcata* (Andersson 1991: 140), from a male collected near Umtali, South Africa, but Stuckenberg (1963) recognised this specimen as the, until then, unknown male of *L. africana*. Séguy (1938) described *L. acinaris* from five specimens from Mt Kenya and two from Mt Elgon, Kenya. Later, Stuckenberg (1963) added two species, *L. transvaalensis* (description based on a single female) from the Drakensburg escarpment near Mariepskop, South Africa and *L. vesperis* (description based on 31 specimens) from the Drakensburg of KwaZulu-Natal Province, South Africa. A further 11 male and 12 female specimens are known from the type locality (Whittington, unpubl.) and a single female specimen was collected in Grahamstown Botanical Gardens, South Africa in 2006 (A.H. Kirk-Spriggs, pers. obs.). Whittington (1991) based the new species *L. rava* on 26 specimens (only 1 male) from inland KwaZulu-Natal Province and *L. ugandensis* (based on two females) from Uganda. In addition, both Stuckenberg (1963) and Whittington (1991) included *L. bifurcata* (as *L. furcata*) in identification keys, believing that this virtually cosmopolitan species would eventually become established in the Afrotropical Region. The synanthropic *L. bifurcata* has since been recorded in the region and has evidently been present for some years. A series of 44 female specimens of *L. bifurcata* was recorded from Réunion Is. by Kassebeer (2002), which were thought to have been introduced by human activities. An additional 76 specimens (all female), were collected from Réunion Is. in 2015 by the junior author, where most specimens were collected from submontane secondary rainforest and rather fewer from urban areas, roadsides and cultivated or cattle pastures. Furthermore, this species is here confirmed from the continental Afrotropics by previously overlooked specimens from South Africa, the earliest known being collected in the Cape Province, South Africa at Orange Grove Farm, near Worcester and from Harkerville Forest Reserve, near Knysna in 1972 by van Reenen & Mathabathe (specimens in the KwaZulu-Natal Museum). Further specimens are known from Van Reenen, KwaZulu-Natal Province collected in 1984; De Rust, Western Cape Province collected in 1990 and from newly collected material on farms near Harrismith, Free State collected in 2009. Biology and immature stages of Afrotropical species remain unknown. An identification key to Afrotropical species (divided into males and females) was provided by Stuckenberg (1963), which was expanded by Whittington (1991), to include the virtually cosmopolitan *L. bifurcata*.

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PHORIDAE 59

(Scuttle Flies)

R. Henry L. Disney

Fig. 59.1. Female of *Ritchiephora diplopodae* Disney (Namibia) (photograph © S.A. Marshall).

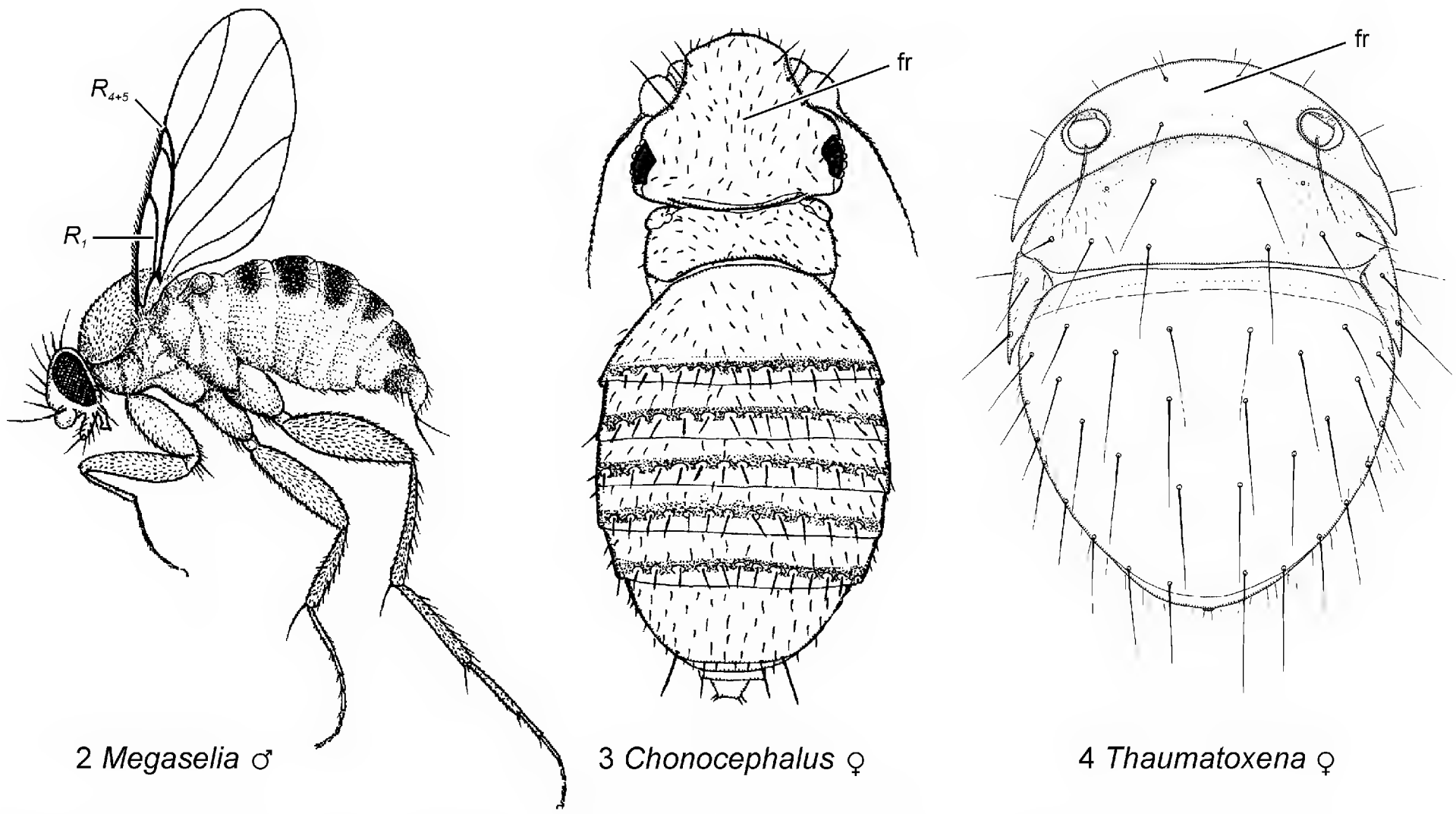
Diagnosis

Small- to minute-sized flies (body length: 0.5–5.5 mm) (Fig. 1), blackish, brownish or yellowish in colour, with conspicuous, backwardly directed head setation (Figs 1, 15, 16) or greatly reduced or absent (Figs 8, 14); frons with median furrow (Figs 10–12) or this lacking; in winged adults venation strikingly reduced (Figs 72–99), with markedly shortened costal vein (*C*) and radial veins and medial veins thinner and finer, with veins M_1 and M_2 unattached basally; some adults stenopterous (Figs 4, 100–112), or with wings entirely absent (Figs 3, 64); flightless adults recognised to be phorids by enlarged conus (apical swelling) of antennal pedicel, enclosed by postpedicel (Fig. 27); arista normally 3-articled (*e.g.*, Figs 30–33), but occasionally the number may be reduced or arista entirely absent; ptilinal-like fissure normally absent, except in genus *Aenigmatistes* Shelford (Fig. 6); hind tibia with 0 (Fig. 170) to several rows of palisade setae (Figs 156, 164, 171); hind tarsomere 1 with 1–4 transverse rows of setae or ctenidia (Fig. 161) or these lacking.

Head of male (Figs 6, 8, 10, 14, 15, 19–21) and female (Figs 5, 7, 9, 11–13, 16–18), small, sometimes rather short or flattened; compound eye usually moderately large (Figs 2, 6–8, 10–12, 14–16), but sometimes small, especially in brachypterous or wingless forms (Figs 3–5, 9, 13, 17), bare or setulose; ocelli usually present (Figs 6–8, 10–12, 14–16, 18–21), but reduced or absent in some apterous females (Figs 3–5, 9, 13); antenna of males (Figs 23, 24, 26, 31, 33, 35, 37, 38, 42, 43, 45) and females (Figs 25, 27–30, 32, 36, 39, 40, 41, 44), with scape and pedicel small and obscured by large postpedicel (Fig. 27); postpedicel globose, oval, pyriform, conical, or retort-shaped, sometimes greatly enlarged or varying in size and shape between sexes; arista apical (Figs 23, 25, 26, 36) sub-apical (Figs 24, 29, 32–35, 37, 40–45), or dorsal (Figs 27,

28, 38, 39) in position, rarely absent, composed of 2 basal articles and long, usually more or less pubescent, third article; frons (Figs 3–16) generally wide, but varying in length, with or without median longitudinal median furrow (coronal suture) (Figs 10–12); frons and vertex typically with conspicuous setae arranged in 3 transverse rows (Fig. 12), comprising 4 setae in each; these setae sometimes supplemented by additional setae, or reduced in number and sometimes weak or absent; uppermost row (when complete), consisting of long inner and short outer vertical setae and pair of long postocellar setae; 2–4 strong or weak supra-antennal setae (sometimes referred to as post-antennal setae), proclinate, porrect, or reclinate, usually present anteromedially just above antennae, sometimes with 1 or more pairs of supernumerary setae, or these entirely absent; ventral row of setae with 2 middle setae, termed lower interfrontal (antial) setae (Fig. 12); presence or absence, position and direction of inclination of supra-antennal and lower interfrontal setae taxonomically important; face short, concave; subcranial cavity large; lower facial margin and clypeus sometimes enlarged and distinctively shaped (especially in female); proboscis (Figs 46, 49, 55, 58, 62, 63) large or small, fleshy and retractile, or produced, sclerotised and non-retractile; palpus usually large (Figs 47, 48, 51–61), sometimes greatly lengthened (Figs 62, 63), often with strong setae.

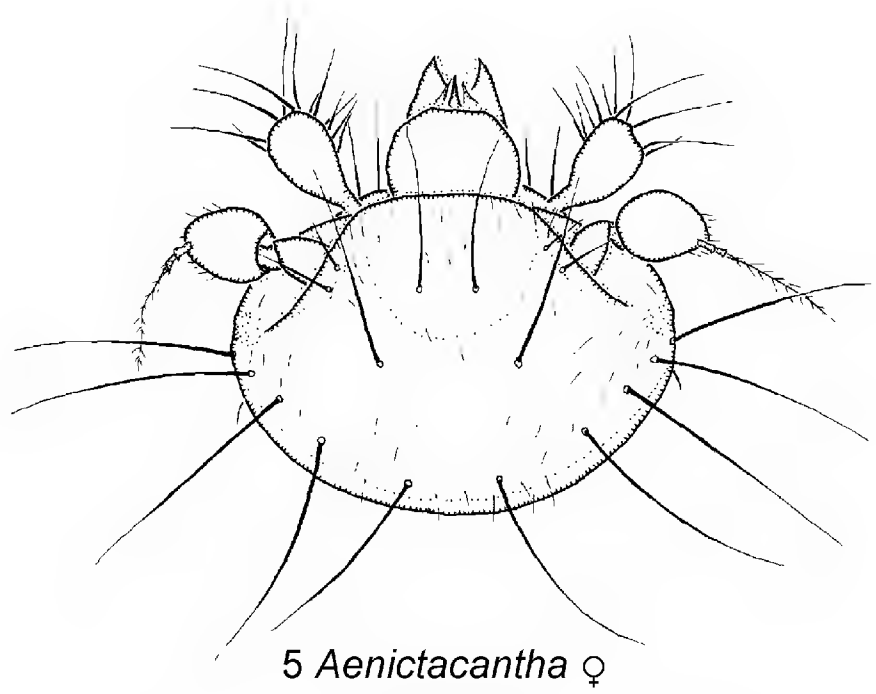
Thorax large, usually arched, giving characteristic humpbacked appearance (Figs 1, 2), but sometimes reduced or somewhat flattened (Figs 68, 70); scutum setulose, not strongly setose, but usually with 1 postpronotal seta, 2–4 notopleural setae (Fig. 68), 1 or 2 supra-alar setae and 1–3 postsutural dorsocentral setae present; occasionally 1 presutural seta and 1 postsutural intra-alar seta present; acrostichal setae short, but sometimes longer, seta-like, especially anterior to scutellum; proepistemum with or without scattered setae, usually with 2–8 ventral and similar number of dorsal setae; anepisternum sometimes divided by dorsoventral anepisternal ridge into anterior and posterior parts (Fig. 66), bare or setose, sometimes with one or more setae posterodorsally; remainder of lateral portions of thorax bare. Scutellum usually clearly defined, but small or absent in some apterous forms (Figs 3, 4), bare or setose above, usually with 2–4 (0–6) setae; anterior pair of scutellar setae (if present), often weak and setula-like. Wing usually large and present in both sexes (Figs 72–99), but female of some species brachypterous or apterous (Figs 3, 4, 100–112); venation distinctive for family (Fig. 72); costal vein (*C*) strong, extending *ca* ½ length of wing, sometimes swollen along entire length or only basally or apically, usually fringed with short to long setae (Fig. 72); subcostal vein (*Sc*) usually short, free or merged apically or more extensively with vein R_1, sometimes faint or absent (Fig. 72); veins R_1 and R_{4+5} strong, crowded toward costal margin (Fig. 72); radial sector (*Rs*) simple (R_{4+5}) or with anterior fork (R_{2+3}), ending in, or very close to tip of costal vein (Fig. 72); remaining veins (M_1, M_2, M_4 and *CuA+CuP*) thin and weakly developed (Fig. 72); M_1 and M_2 often free at base, not directly connected to basal venation of wing (Figs 72, 74, 81, 83); several tiny, pore-like sensory organs



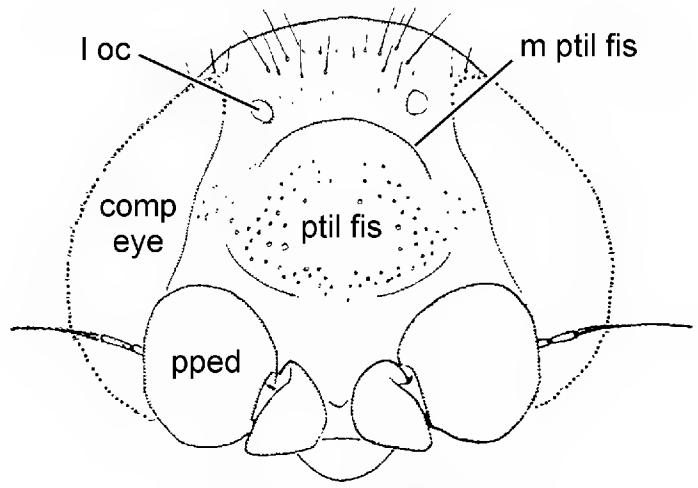
Figs 59.2–4. Habitus of Phoridae: (2) *Megaselia scalaris* Loew, lateral view ♂; (3) *Chonocephalus dominicanus* Borgmeier, dorsal view (legs omitted) ♀; (4) same, *Thaumatoxena andreinii* Silvestri. Fig. 2 (courtesy J. Rodford), Figs 3, 4 (Disney 1994, figs 6.7, 8.90).

Abbreviations: fr – frons; R_1 – anterior branch of radius; R_{4+5} – third branch of radius.

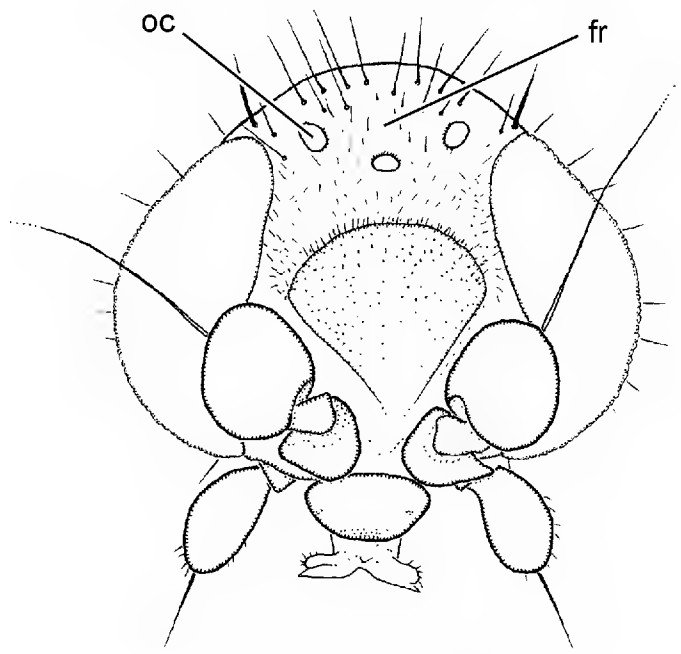
not associated with setae present at various places on anterior veins; a distributional pattern generally evident, but exact locations and numbers varying considerably (function or taxonomic significance unknown); halter usually present (Fig. 70), but absent in some wingless forms. Legs (Figs 122–173) usually well-developed; hind femur usually stout (Figs 145–148, 150, 158–160, 162, 167), often enlarged and more or less laterally compressed (Figs 144, 149; 151–153, 155–157, 163); various



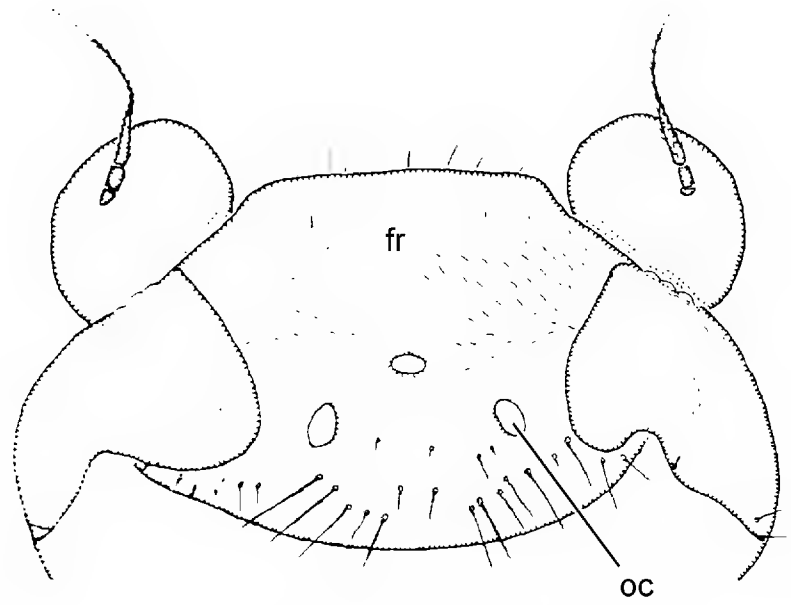
5 *Aenictacantha* ♀



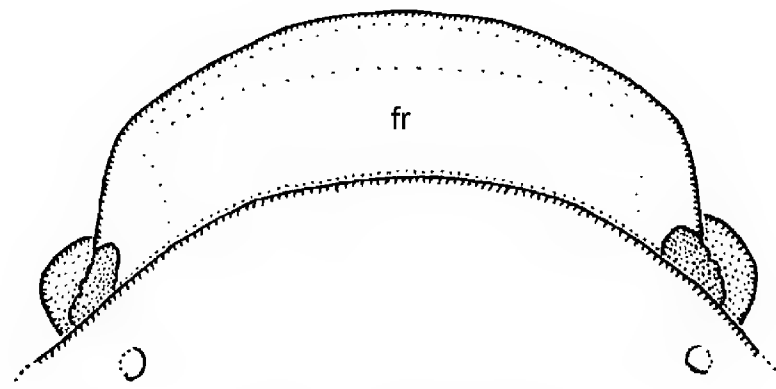
6 *Aenigmatistes* ♂



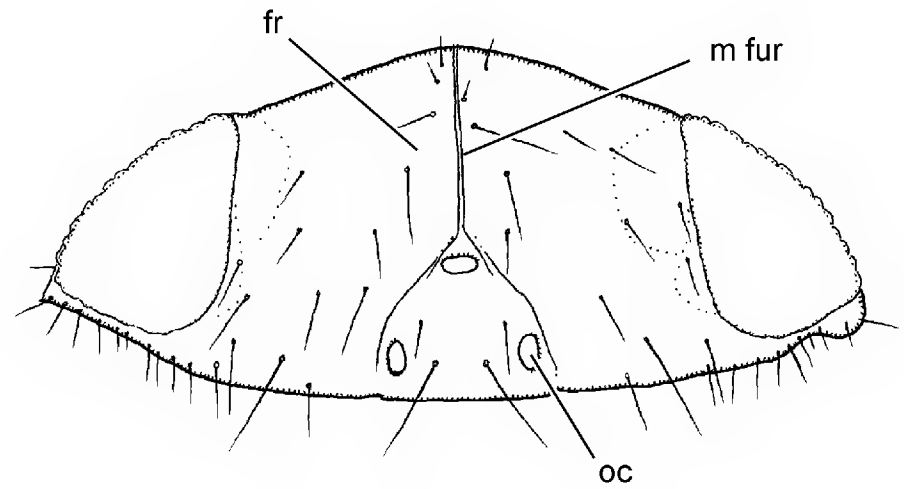
7 *Aenigmatistes* ♀



8 *Aenigmatistes* ♂



9 *Aenigmatistes* ♀



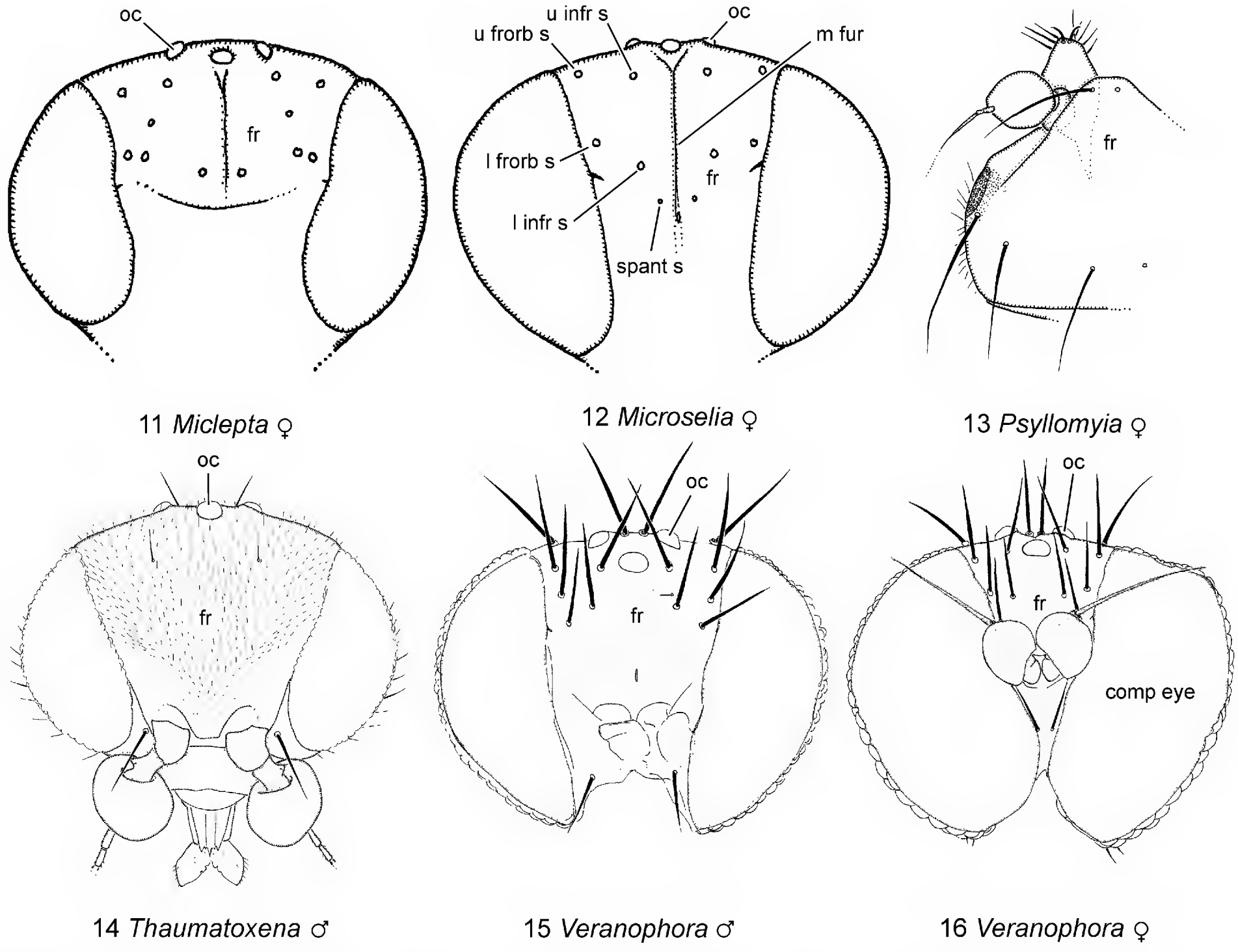
10 *Danumphora* ♂

Figs 59.5–10. Heads of Phoridae: (5) *Aenictacantha setifera* Disney, frontal view ♀; (6) same, *Aenigmatistes foveolatus* Schmitz ♂; (7) same, *Aenig. scutellatus* (Becker) ♀; (8) *Aenig. foveolatus* Schmitz, dorsal view ♂; (9) same, *Aenig. scutellatus* (Becker) ♀; (10) same, *Danumphora hageri* Disney ♂. Figs 5, 6, 8 (Disney 1994, figs 8.20a, 1.4b, 1.4a, respectively), Figs 7, 9, 10 (Disney 2006, figs 2, 3, 28).

Abbreviations: comp eye – compound eye; fr – frons; l oc – lateral ocellus; m fur – median furrow; m ptil fis – margin of ptilinal fissure; oc – ocellus; pped – postpedicel; ptil fis – ptilinal fissure.

sensory organs sometimes present on inner (posterior) surface at base of hind femur (Figs 151, 155) and less frequently on mid femur of male; tibiae, in addition to one or more apical setae, with or without strong isolated setae; often hind tibia and sometimes mid tibia with 1 or 2 dorsal palisade setae (Figs 156, 164, 171), composed of short closely set setae; a row of longer posterodorsal setae also usually present; ctenidium of short setae sometimes present on tibiae and tarsi of mid and hind legs.

Abdomen (Figs 2–4, 64) well-developed, somewhat conical and more or less tapered posteriorly, usually with 3–6 tergites, but often mostly membranous, especially in wingless forms; 7 spiracles usually present; male terminalia (Figs 176, 178–218) small to large in relation to abdomen, usually asymmetrical and highly complex; epandrium (Figs 176, 178–182, 193) usually large, but sometimes reduced, with one side sometimes more reduced than the other, causing variation in shape as well as in size, sometimes simple or with secondary lobes or secondary process; surstylus (Figs 182, 196, 197) highly variable both in size and shape, often exhibiting considerable variation from side to side, sometimes with one or more secondary lobes or processes; hypoproct (Figs 184, 185) heavily sclerotised, varying in size, shape and complexity; anal tube (cercus and hypoproct combined) varying from absent or greatly reduced to greatly elongate, usually tube-like, with or without setae; when anal tube developed, cerci demarcated at apex (Fig. 176); cercus (Figs 182, 184, 185, 193, 196, 197) usually small, but sometimes quite large; hypandrium (Figs 182, 193) variable in size, broadly U-shaped usually, but often asymmetrical; usually with distinct, but variably developed phallic guide and sometimes with lobe-like, plate-like, or spiniform processes probably representing gonopods (Figs 182,



Figs 59.11–16. Heads of Phoridae: (11) *Miclepta arrujumensis* Disney (setae represented by sockets only), frontal view ♀; (12) same, *Microselia yemenensis* Disney; (13) *Psyllomyia braunsi* Schmitz, left dorsal view ♀; (14) *Thaumatoxena andreinii* Silvestri, frontal view ♂; (15) same, *Veranophora medleri* (Disney) ♂; (16) same ♀. Figs 11, 12 (Disney 2006, figs 60, 64), Fig. 13 (Disney & Kistner 1998, fig. 18), Figs 14–16 (Disney 1994, figs 8.89a, 8.27b, 8.28a, respectively).

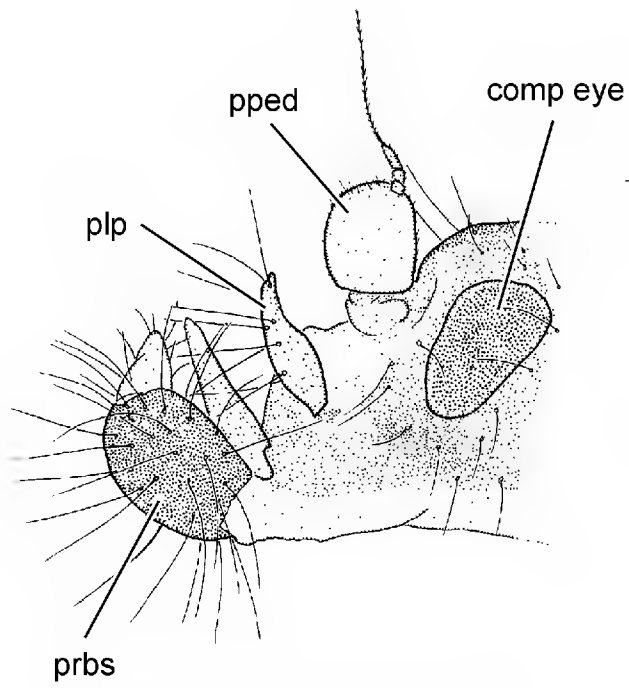
Abbreviations: comp eye – compound eye; fr – frons; l frorb s – lower fronto-orbital seta; l infr s – lower interfrontal seta; m fur – median furrow; oc – ocellus; spant s – supra-antennal seta; u frorb s – upper fronto-orbital seta; u infr s – upper interfrontal seta.

196, 197); phallic processes usually well-developed, but varying in size and shape, often complex and asymmetrical, often situated in dorsolateral and ventrolateral position; sperm pump and ejaculatory apodeme, if present, unsclerotised and not discernible; phallus (Fig. 182) correspondingly complex, usually rather short, broad and mostly membranous; membrane with minute spicules and variously shaped sclerites and often with variably short to elongate slender sub-apical spine-like process, that may be somewhat membranous or sclerotised; phallapodeme usually short, but often well-developed; female of some species with dorsal gland openings on segment 5 or 6; ovipositor small and fleshy; tergite 7 sometimes stiffened by sclerotised rod; small apparent tergite 9 and epiproct sometimes present, or these large, corneous and adapted for piercing; sternite 9 internalised and ovipositor may be elongated and embraced by a sheath when withdrawn; sternites 1–6 typically absent, but rarely 6 present (Figs 174, 225) and sternite 8 (the furca) internalised (Figs 220–221); in Gymnophorini Dufour's crop mechanism present at anterior end of crop and in some elaborate and heavily sclerotised (Fig. 22); 1 non-sclerotised spermatheca in three species of two genera of Phoridae.

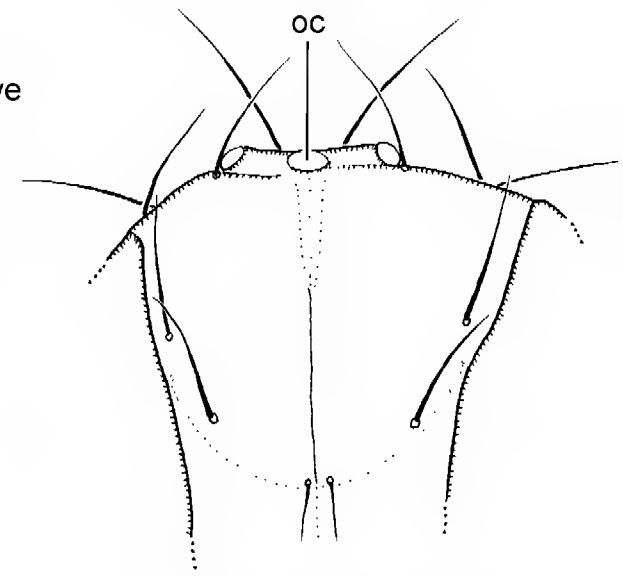
Adult Phoridae are superficially similar to several flies that are less than 6 mm in length. However, the simplified wing venation immediately excludes most families of Diptera, except some lower Diptera, the bead-like antennae of which immediately differentiates them. For other small Diptera, the presence of abdominal sclerites excludes the Phoridae, except for the exceptions noted above. The latter's antennae will distinguish them from these flies. With the flightless Phoridae, the lack of abdominal sclerites and the antennae will distinguish them.

Biology and immature stages

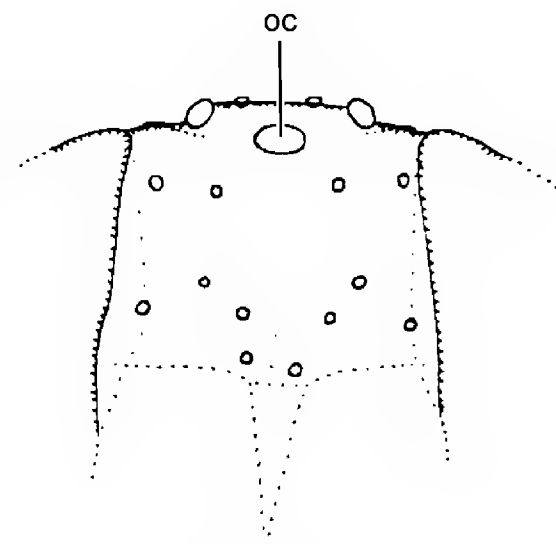
Eggs are typically elongated with the outer surface smooth (Fig. 252) or with varied micro-sculpture. Some with a



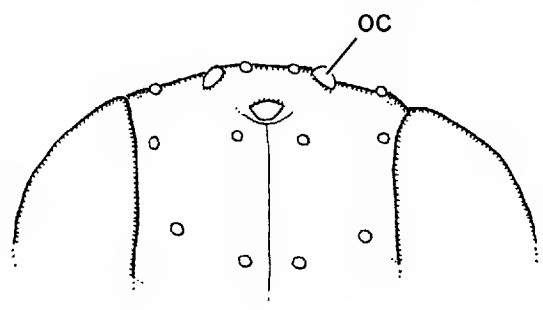
17 *Syntermitoxenia* ♀



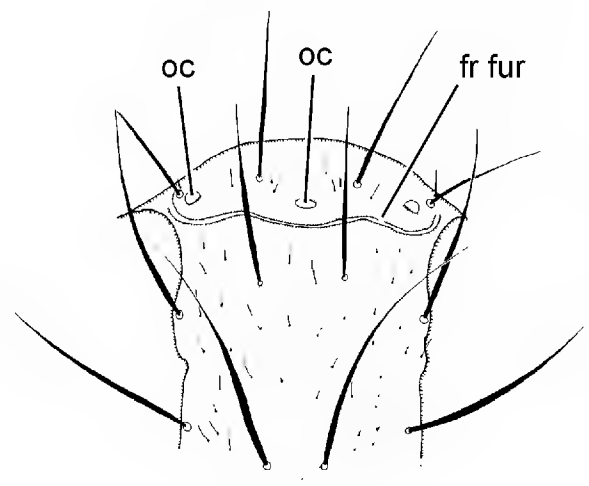
18 *Epactoselia* ♀



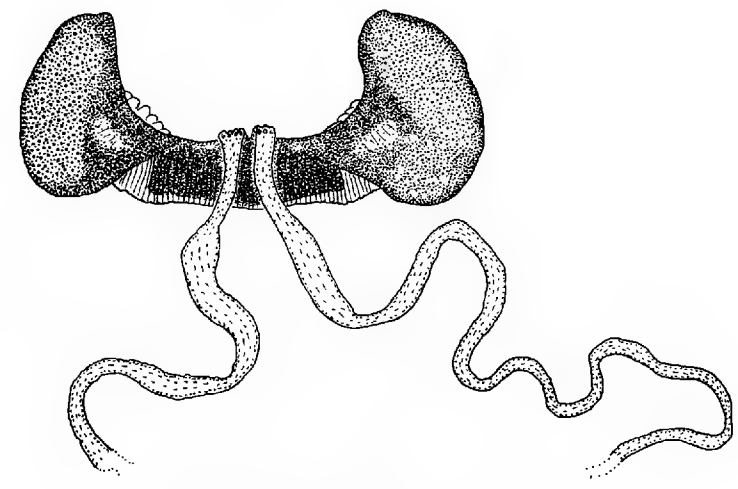
19 *Haulepta* ♂



20 *Ritchiephora* ♂



21 *Stichillus* ♂



22 *Woodiphora* ♀

Figs 59.17–22. Head, frons and internal features of Phoridae: (17) front half of head of *Syntermitoxenia extra* Disney, left lateral view ♀; (18) frons of *Epactoselia provallaris* Disney, dorsal view ♀; (19) same, *Haulepta sheasbyi* Disney (setae represented by sockets only), dorsal view ♂; (20) same, *Ritchiephora diplopodae* Disney ♂; (21) same, *Stichillus* sp. ♂; (22) internal Dufour's crop mechanism of *Woodiphora collini* Disney, ventral view ♀. Fig. 17 (Disney & Kistner 1995, fig. 52), Fig. 18 (Disney & Kistner 1998, fig. 8), Fig. 19 (Disney & Kistner 1997, fig. 8), Fig. 20 (Disney & Ritchie 1997, fig. 1), Fig. 21 (Disney 1994, fig. 8.94d), Fig. 22 (Disney 2009*b*, fig. 179).

Abbreviations: comp eye – compound eye; fr fur – frontal furrow; oc – ocellus; plp – palpus; pped – postpedicel; prbs – proboscis.

well-developed plastron (*e.g.*, Fig. 251). Typically, there are three larval instars, but at least in some "Termitoxeniinae" only the final instar may be briefly free-living, as opposed to being retained within the greatly enlarged eggs. Furthermore, the adult female continues to grow following eclosion, exhibiting a remarkable heterochrony (Disney 1997). A typical larva is illustrated in Fig. 254, with details of the cephaloskeleton in Figs 255–257. The puparium (Fig. 258) usually bears a pair of eclosion plates, each of which is pierced by a pupal respiratory horn (Figs 258, 259), but the plates are sometimes fused to each other and to the anterior cap.

The larval habits of Phoridae are more varied than those of any other family of insects (Disney 1994). Indeed, the range of larval habits in the massive genus *Megaselia* Rondani is at least as wide as that of the family as a whole. The larval habits of Afrotropical Phoridae are largely unknown, however. The following few reports underline the extent of our ignorance on the subject. The larvae of some *Megaselia* species have been recorded in the axil waters of Coconut palms, *Cocos nucifera* L. (Arecaceae) (Haworth 1924). Larvae of *Wandolleckia achatinae* Cook, 1897, feed on the dung of snails of the genus *Achatina* Lamarck (Achatinidae) (Baer 1953). Vertebrate dung is exploited by *Megaselia scalaris* Loew, 1866; the larvae of which also feed on dead Arthropoda, other invertebrate and vertebrate carrion, including human corpses and thus feature in forensic investigations (Disney 2008*a*). Likewise, the larvae of *M. curtineura* Brues, 1909 not only feed on dead Arthropoda, Mollusca, *etc.*, but have been reported from human corpses in Malaysia (Thevan *et al.* 2010) and similarly with *Dohrniphora cornuta* (Bigot *in* de la Sagra, 1857) has been reported in forensic cases elsewhere (Disney *et al.* 2013*b*). *Megaselia rufipes* (Meigen, 1804) not only feeds on a range of decaying organic matter, but is frequent in forensic cases involving human corpses in Europe (Disney 1994: 35, 2005*b*), but its infrequent occurrence in the Afrotropical Region probably represents accidental introductions by humans. The larvae of several other species feed on dead Arthropoda and/or Mollusca (Disney 1994: 62). Among such species recorded from the Afrotropical Region are the following: *Gymnoptera simplex* (Brues, 1905), *Plethysmochaeta trinervis* (Schmitz, 1915), *Puliciphora borinquenensis* Wheeler, 1906 and *Pu. rufipes* Silva-Figuero, 1916. *Megaselia rufipes*, *M. scalaris*; *Pl. trinervis* and *Pu. borinquenensis* have also been reared from fish baits in Nigeria (Disney 1995*a*). Adults of *Beyermyia spinulicosta* (Beyer, 1965) have been recorded at carcasses of Impala, *Aepyceros melampus* (Lichtenstein) and Springbok, *Antidorcas marsupialis* (Zimmermann) (both Bovidae) (Disney 1991*e*).

Some species are fungus-feeders (*e.g.*, Disney *et al.* 2013*a*), including pests of cultivated mushrooms (see "Economic significance" below). These include feeders on the fungus combs of *Termitomyces* species (Amanitaceae) in termitaria, such as *Dohrniphora diminuens* (Schmitz, 1935) (Disney & Kistner 1989). The sporophores of these fungi are exploited by a different suite of species, such as *Megaselia labiata* Borgmeier, 1967 (= *M. termitomyca* Disney, 1989) and *M. zariaensis* Disney, 1989 (Disney 1989*a*). Decaying fungus sporophores are exploited by other species, such as *M. scalaris* (Disney 2008*a*) and *Chonocephalus fletcheri* Schmitz, 1912 (Disney 2005*a*).

Several species of *Chonocephalus* Wandolleck have been reared from fruits, such as Moracaeae and Palmaceae, or from rotting plants, such as *Hibiscus* (Malvaceae) (Disney 2005*a*) and a decomposing Pawpaw tree, *Carica papaya* L. (Caricaceae) (Disney 1991*c*). Five species of *Megaselia* have been reared from figs, *Ficus* species (Moraceae) (Compton & Disney 1991). The larvae of *Metopina ciceri* Disney, 1988 feed on the root nodules of Chickpea, *Cicer arietinum* L. (Fabaceae) (Disney 1988).

Many phorid larvae are parasitoids, but only a few reports relate to Afrotropical species. *Microselia deemingi* Disney, 1983, was observed attempting to oviposit on the carpenter ant *Camponotus acvapimensis* Mayr (Formicidae), attending a colony of the scale *Udinia catori* (Green) (Coccidae) on the tree *Cussonia barteri* Seem (Aralaceae) (Disney 1983*a*). *Dohrniphora isopterorum* Disney, 2000 larvae parasitise alate termites of both sexes of the genus *Odototermes* Holmgrem (Termitidae) (Disney & Darlington 2000*a*). *Ritchiephora diplopodae* Disney, 1997, parasitises millipedes (Fig. 1) (Disney & Ritchie 1997). *Razorfemora zaragozae* Disney, 2006 parasitises the ant *Messor barbarus* (L.) (Delgado *et al.* 2020).

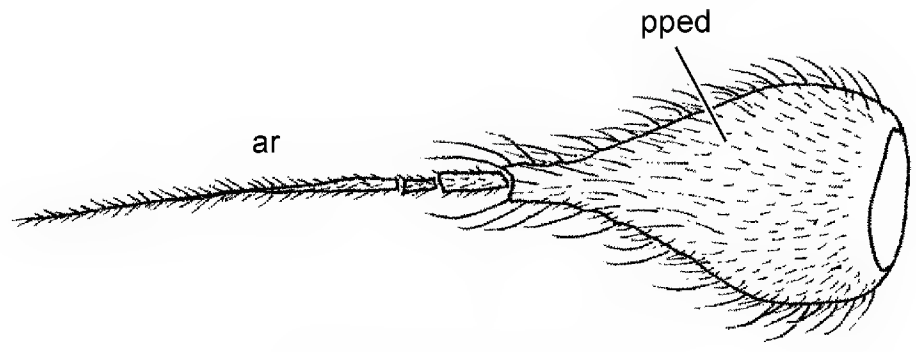
Megaselia species have been reared from the egg pods of locusts and other Acrididae (Orthoptera) (Cuthbertson 1936; Jack 1935), but seemingly these are only secondary invaders of already damaged egg pods (Popov 1959). Facultative parasitism of humans by *M. scalaris* include cases of intestinal myiasis in the Afrotropics (*e.g.*, Rhodes-Jones 1957) and urogenital myiasis (*e.g.*, Meinhardt & Disney 1989).

Many Phoridae visit flowers for nectar, or feed on honeydew on leaves, but records for the Afrotropical Region are few, aside from the records of pollinia of *Ceropegia* or other Asclepiadaceae adhering to the proboscis of *Megaselia curtineura*, *M. media* Collin, 1912, *M. microcurtineura* Disney, 1991, *M. orgaoa* Disney, 1991 and *M. senegalensis* Disney, 1980 (Disney 2009*c*), as well as other undescribed female *Megaselia* (Heiduk *et al.* 2017). Some females ingest fungal spores, which are dispatched to the crop, *e.g.*, *M. harteni* Disney, 1991 and the crop of a female *M. jorgensis* Disney, 1991 has been reported to contain small, flattened setulae, probably of Arthropoda origin (Disney 1991*c*).

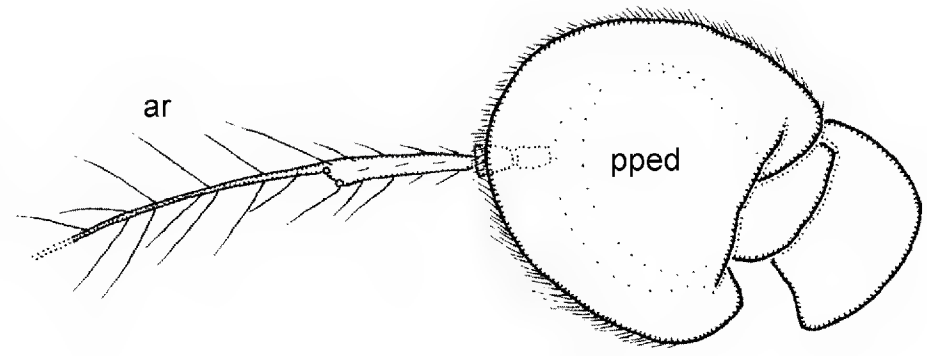
Females of some Phoridae prey on other insects and in the Afrotropics *Megaselia parvorata* Disney, 1991 and *M. vorata* Disney, 1991 are recorded as preying on newly emerged fig wasps (Hymenoptera: Agaonidae) (Compton & Disney 1991). *Termitosagma henningsi* Reichensperger, 1931 females steal food from the nymphs and younger larvae of their termite hosts (Kistner 1982; Malin & Kistner 1970).

Adults, chiefly males, of *Megaselia equitans* Schmitz, 1939 occur on the backs of the large millipede *Archispirostreptus transmarinus* Hoffman (Spirostreptidae) (Schmitz 1939) and likewise males of *M. audreyae* Disney, 1978 on the backs of the large *Pachybolus* Cook (Pachybolidae) millipedes (Disney 1978).

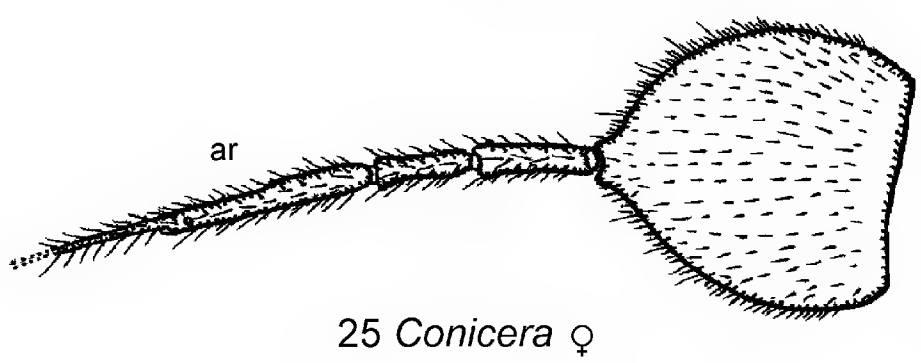
Many species with adult females that inhabit colonies of ants and termites are flightless, being transported by the winged males to the host colonies during nuptial flights (Disney 2005*a*). The mountain-dwelling males of *Aptinandria* Schmitz and *Arrenaptenus* Schmitz are also flightless.



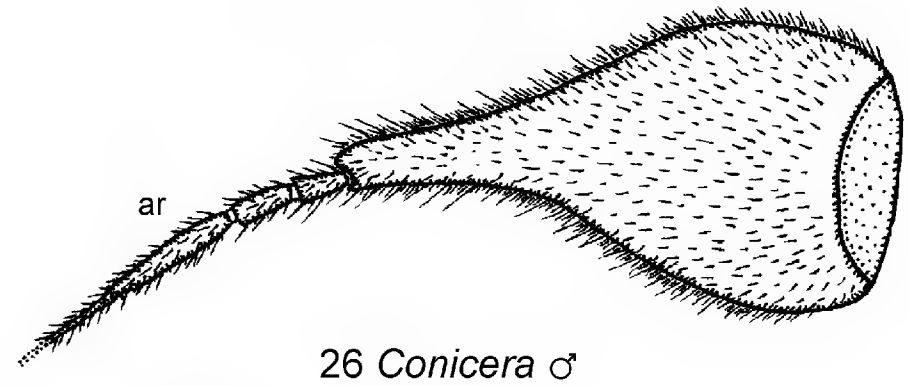
23 *Arababiphora* ♂



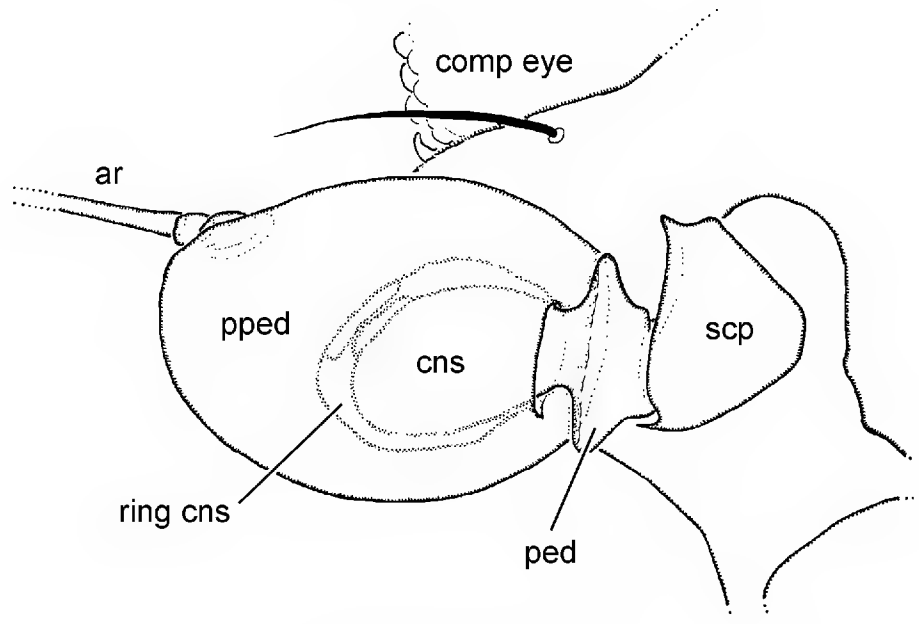
24 *Cheiloxenia* ♂



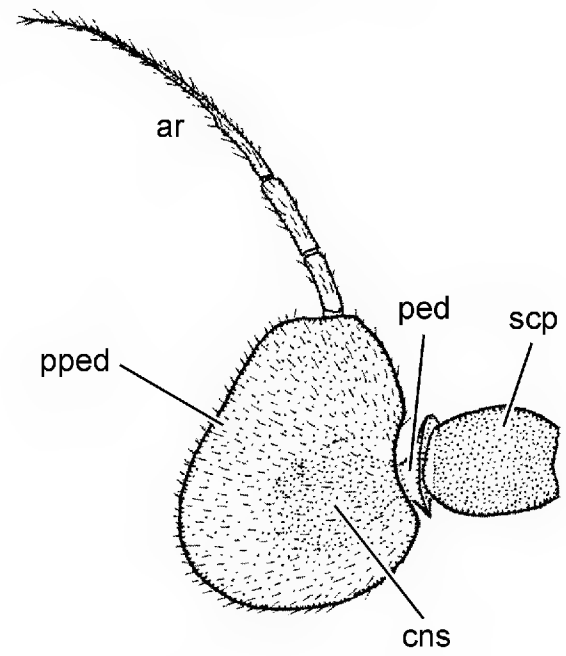
25 *Conicera* ♀



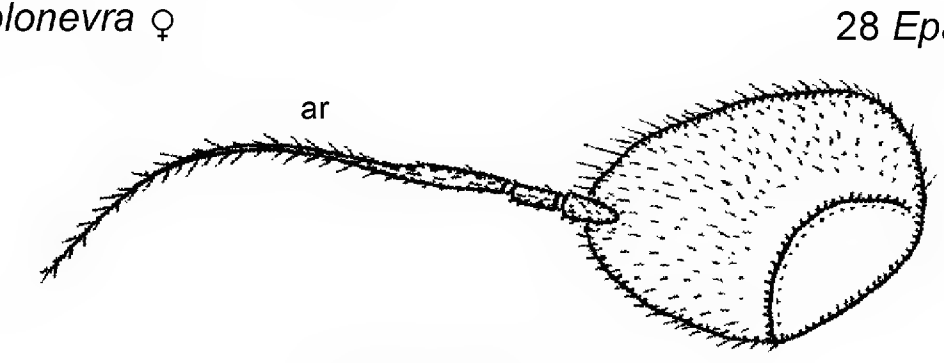
26 *Conicera* ♂



27 *Diplonevra* ♀



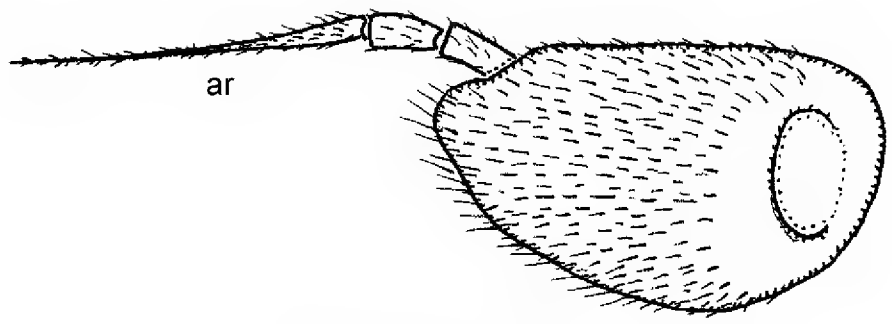
28 *Epactoselia* ♀



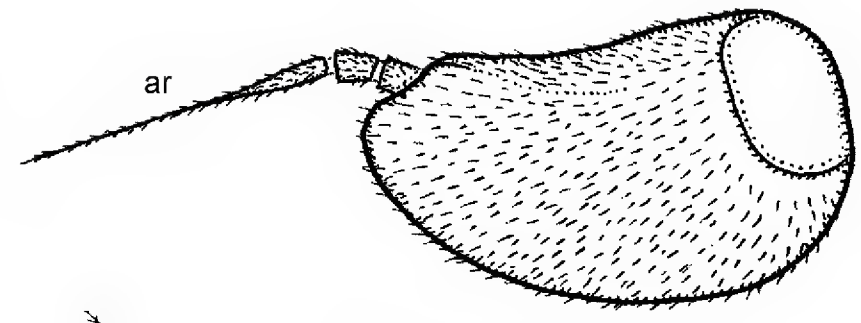
29 *Miclepta* ♀

Figs 59.23–29. Antennal features of Phoridae: (23) postpedicel and arista of *Arabiphora tenuifemorata* Disney, lateral view ♂; (24) antenna of *Cheiloxenia obesa* Delachambre, ventral view ♂; (25) postpedicel and arista of *Conicera tibialis* Schmitz, lateral view ♀; (26) same, ♂; (27) antenna of *Diplonevra* sp., lateral view ♀; (28) same, *Epactoselia provallaris* Disney ♀; (29) postpedicel and arista of *Miclepta arrujumensis* Disney, lateral view ♀. Fig. 23 (Disney 2006, fig. 9), Fig. 24 (Disney & Kistner 1995, fig. 5), Figs 25, 26 (Disney & Aguiar 2008, figs 21, 22), Fig. 27 (Disney 1994, fig. 1.2), Fig. 28 (Disney & Kistner 1998, fig. 9), Fig. 29 (Disney 2006, fig. 62).

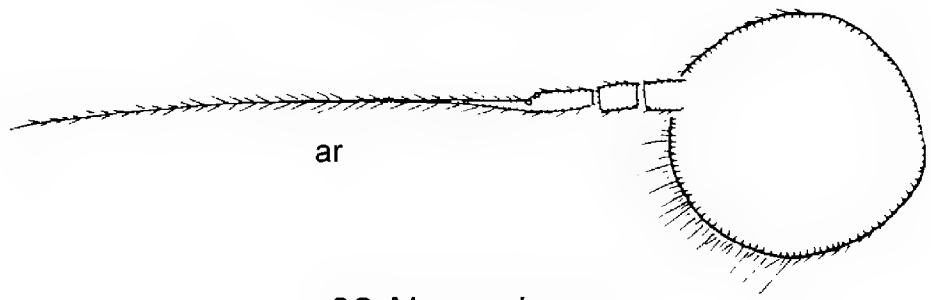
Abbreviations: ar – arista; cns – conus; comp eye – compound eye; ped – pedicel; pped – postpedicel; ring cns – apical ring of conus; scp – scape.



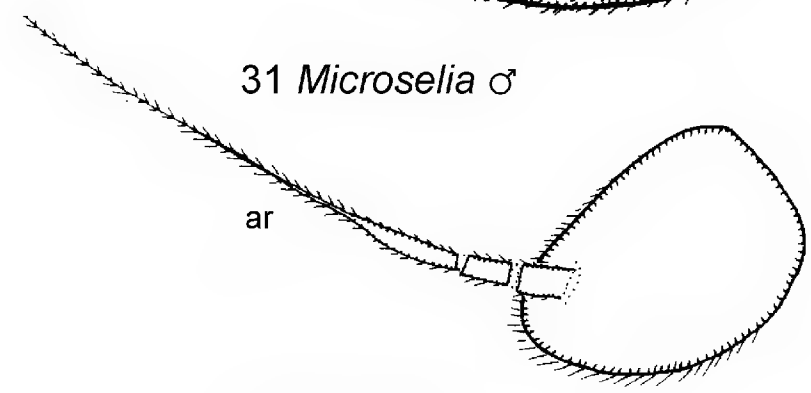
30 *Microselia* ♀



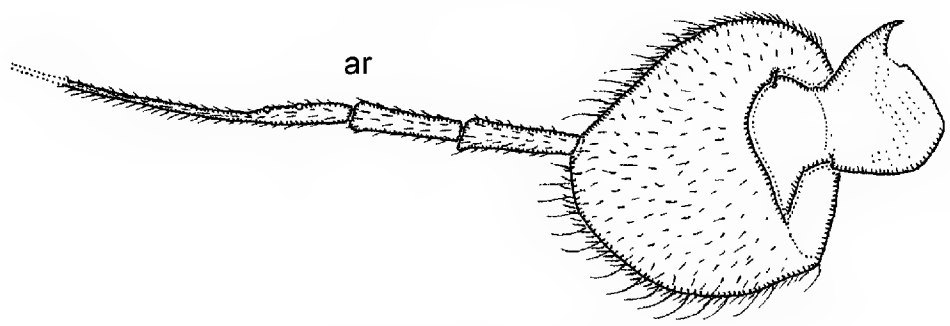
31 *Microselia* ♂



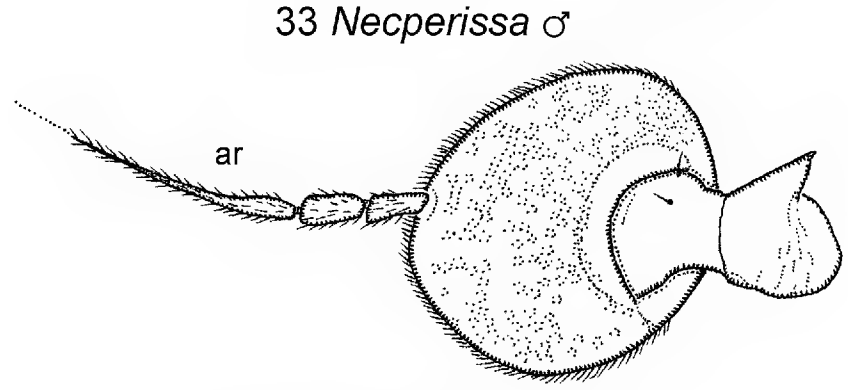
32 *Necperissa* ♀



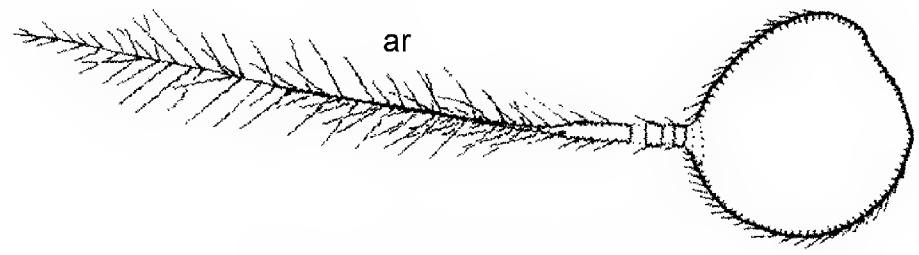
33 *Necperissa* ♂



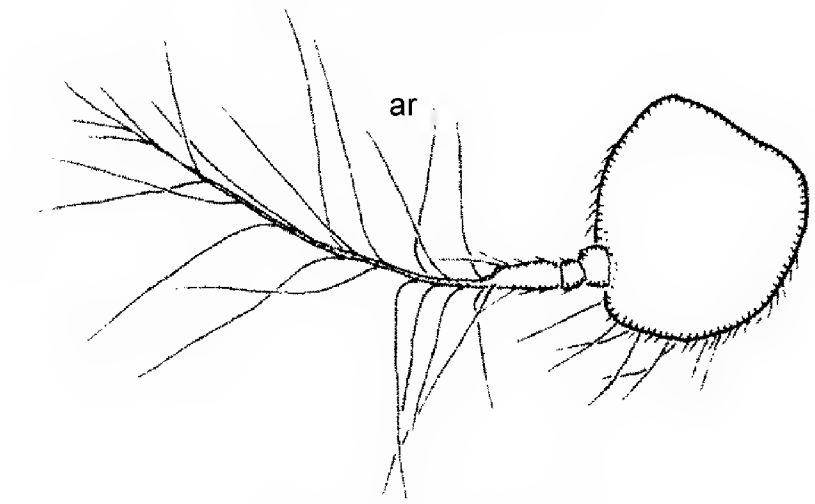
34 *Plastophorides* ♀



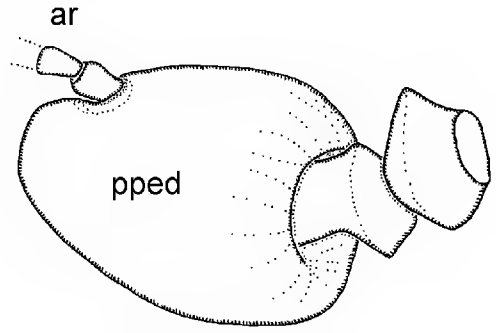
35 *Plastophorides* ♂



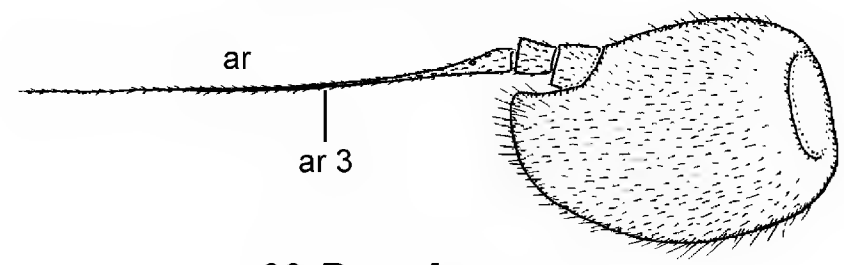
36 *Ptochomyia* ♀



37 *Ptochomyia* ♂



38 *Razorfemora* ♂



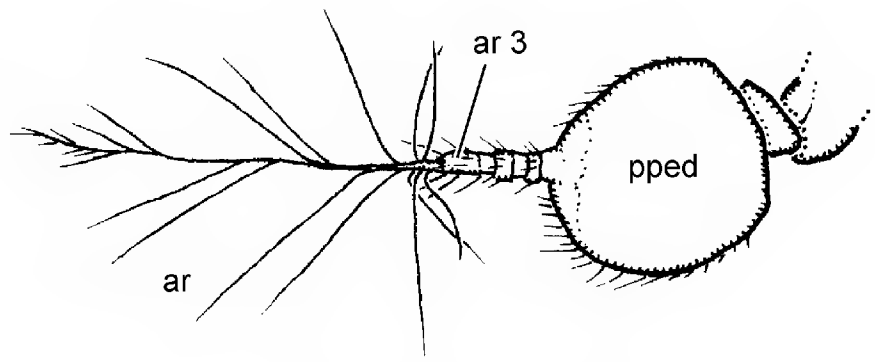
39 *Razorfemora* ♀

Figs 59.30–39. Antennal features of Phoridae (lateral views): (30) postpedicel and arista of *Microselia yemenensis* Disney ♀; (31) same ♂; (32) same, *Necperissa tinglie* (Disney) ♀; (33) same ♂; (34) same, *Plastophorides aculeipes* (Collin) ♀; (35) same ♂; (36) same, *Ptochomyia cummingae* Disney ♀; (37) same ♂; (38) antenna of *Razorfemora nussbaumi* Disney ♂; (39) same, postpedicel and arista ♀. Figs 30, 31, 39 (Disney 2006, figs 66, 67, 89), Figs 32, 33, 37 (Disney & Kistner 1995, figs 15, 16, 42), Figs 34, 35 (Disney 1991a, figs 18, 19), Figs 36, 38 (Disney 1994, figs 8.76b, 8.78e).

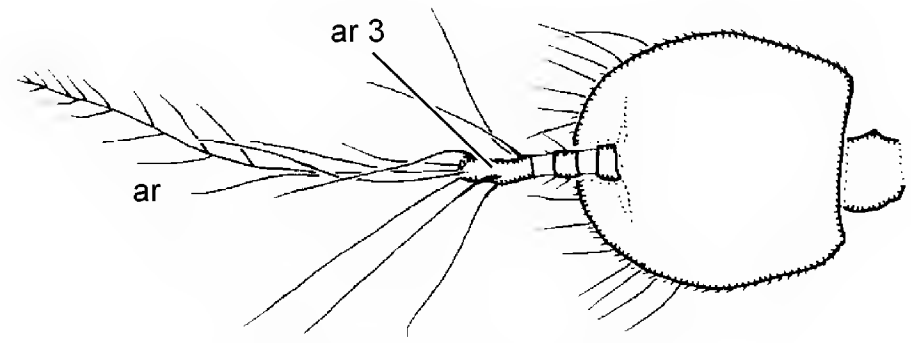
Abbreviations: ar – arista; ar 3 – aristomere 3; pped – postpedicel.

Records of myrmecophiles include: *Aenictacantha crassitarsalis* Disney *in* Disney & Kistner, 1998, with *Aenictus decolor* (Mayr, 1879); *Epactoselia provallaris* Disney, 1998, *Euryplatea eidmanni* Schmitz, 1941 and *Euryphora madagascarensis* Schmitz, 1915, with *Crematogaster* Lund sp.; *Aenigmatopoeus* Schmitz sp., *Conicera* Meigen sp., *Diplonevra brincki* Beyer, 1959, *Dohrniphora* Dahl sp., *Hexacantherophora cohabitans* Schmitz, 1914, *Megaselia furvicolor* Beyer, 1959, *Psyllomyia* Loew sp., *Puliciphora karensis* Disney, 1998 and *Pu. rufipes* in colonies of *Dorylus* F. species; and *Microplatyphora congolensis* Schmitz, 1915 with *Tetramorium aculeatum* (Mayr) (Colyer 1958; Disney & Kistner 1998, 2003; Schmitz, 1915, 1941a, *b*). *Megaselia floccicauda* Disney, 2006, described from United Arab Emirates and Yemen, has subsequently been reported from the nest of a *Camponotus* Mayr species in Palaearctic Bulgaria (Disney & Lapeva-Gjonova 2011).

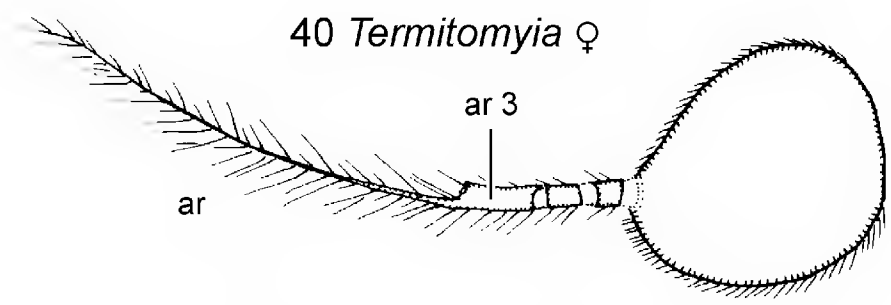
Records of Afrotropical termitophiles include the "Termitoxeniinae" (revised by Disney & Kistner 1995) as follows: *Cheiloxenia obesa* Delachambre, 1966 with the termite *Megaprotermes giffardii* (Silvestri); *Linklloydia ivorensis* (Delachambre, 1965) with *Protermes prorepens* (Sands); *Necperissa tinglei* Disney, 1990 with *Odontotermes lacustris* Haris (Termitidae); *Paratermitoxenia coatoni* Beyer, 1965 with *Allodontermes rhodesiensis* (Sjöstedt); *Ptochomyia afra* Silvestri, 1920 with *Ancistrotermes cavithorax* (Sjöstedt) and *An. crucifer* (Sjöstedt); *Pt. cummingae* Disney, 1993 with *An. latinotus* (Holmgren); *Syntermitoxenia extra* Disney, 1995 and *Sy. jaegerskioeldi* (Wasmann, 1904) with *Odontotermes interveniens* Sjöstedt and *Od. latericius* (Haviland) (*Sy. jaegerskioeldi* also with *Od. lacustris* Harris); *Termitomyia mirabilis* (Wasmann, 1901) with *Od. capensis* (De Geer) and *Od. vulgaris* (Haviland); *Termitophilomyia braunsi* (Wasmann, 1900) with *Od. latericius* and *Od. transvaalensis* (Sjöstedt); *T. gracilis* (Reichensperger, 1931) with *Od. badius* (Haviland), *Od. culturarum* Sjöstedt, *Od. montanus* Harris and *Od. nolaensis* Sjöstedt; *T. leleupi* (Schmitz, 1955) with *Od. okahandjae* (Fuller) and *Od. fulleri* (Emerson); *T. papillacollaris* Disney, 1995 with *Od. transvaalensis*; *T. uvirana*



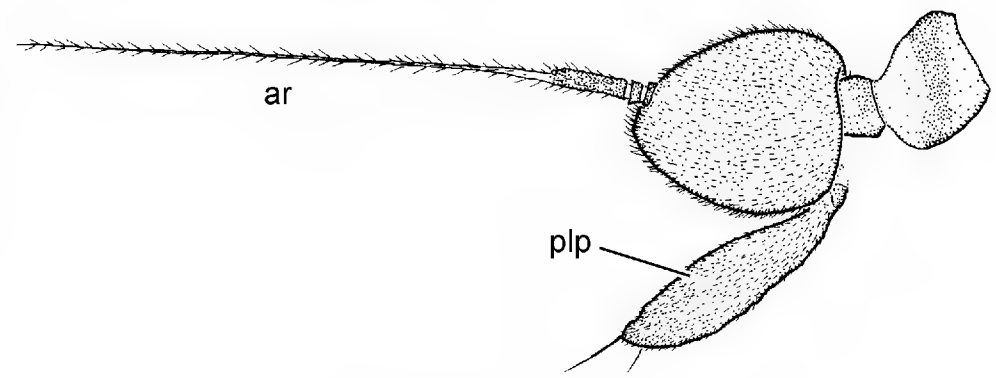
40 *Termitomyia* ♀



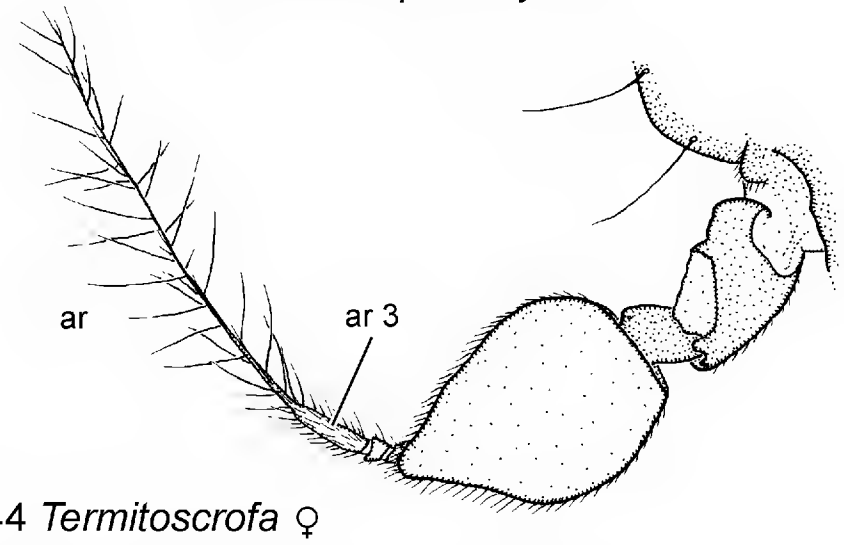
41 *Termitophilomyia* ♀



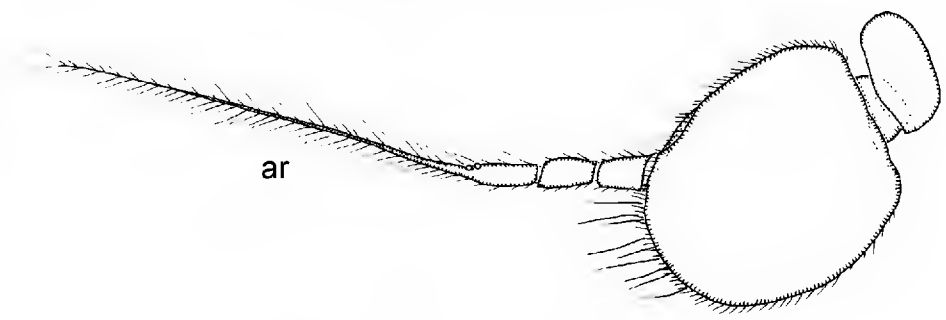
42 *Termitophilomyia* ♂



43 *Termitosagma* ♂



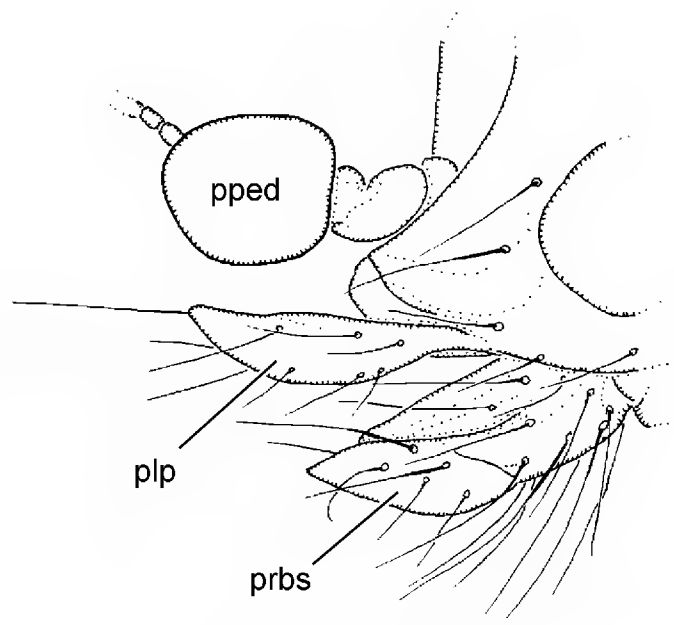
44 *Termitoscrofa* ♀



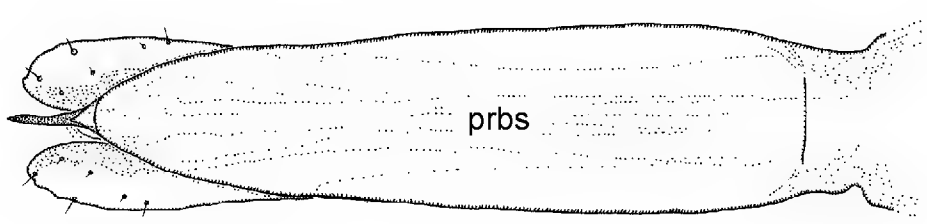
45 *Termitoxenia* ♂

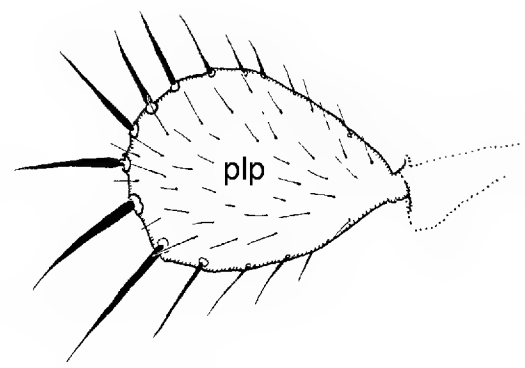
Figs 59.40–45. Antennal features of Phoridae (lateral views): (40) antenna of *Termitomyia mirabilis* (Wasmann) ♀; (41) same, *Termitophilomyia zimbraunsi* Disney ♀; (42) same, postpedicel and arista ♂; (43) palpus and antenna of *Termitosagma henningsi* Reichensperger ♂; (44) antenna of *Termitoscrofa pinguissima* Reichensperger ♀; (45) same, *Termitoxenia oligoseta* (Disney) ♂. Figs 40, 44, 45 (Disney & Kistner 1995, figs 70, 44, 45, respectively), Figs 41, 42 (Disney 1994, figs 8.85a, 8.84b, respectively), Fig. 43 (Disney & Darlington 2000*a*, Fig. 11).

Abbreviations: ar – arista; ar 3 – aristomere 3; plp – palpus; pped – postpedicel.

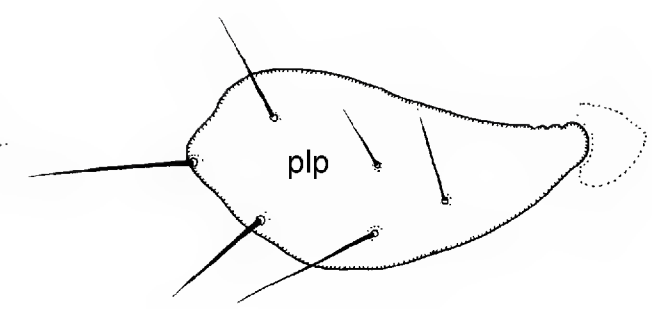


46 *Ptochomyia* ♀

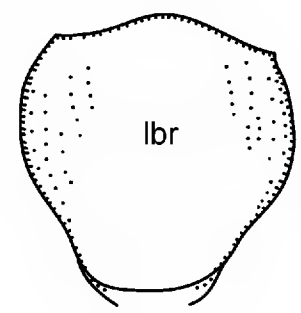


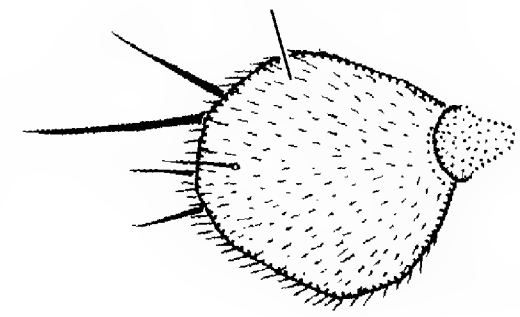


47 *Aenigmatopoeus* ♀



48 *Cheiloxenia* ♀

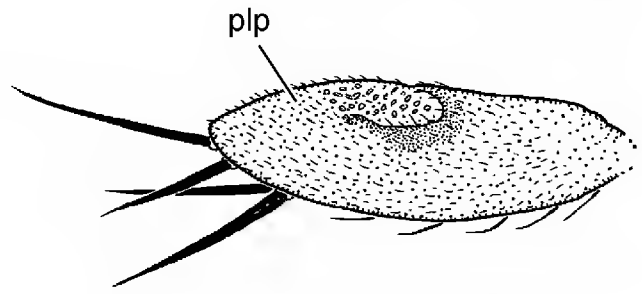


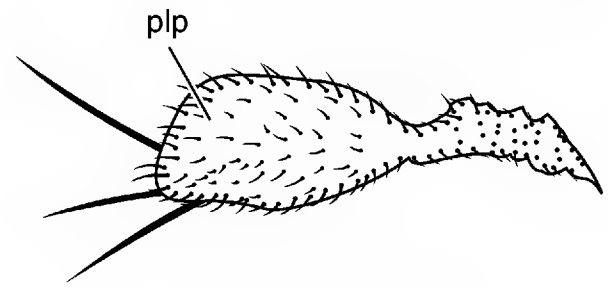


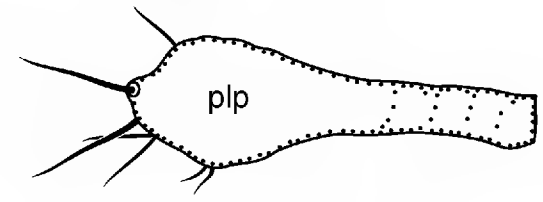
49 *Dohrniphora* ♀

50 *Gymnoptera* ♀

51 *Haulepta* ♂



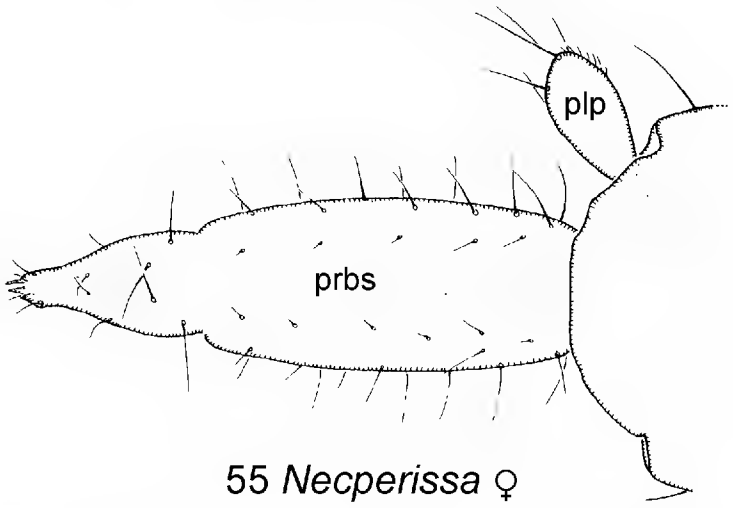


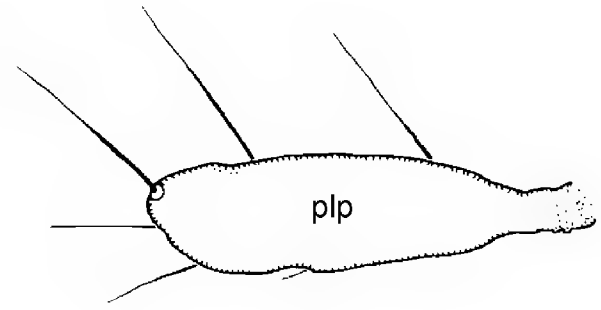


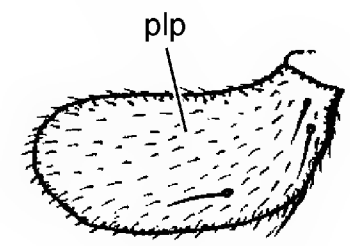
52 *Hypocerides* ♂

53 *Miclepta* ♀

54 *Microselia* ♀







55 *Necperissa* ♀

56 *Perittophora* ♀

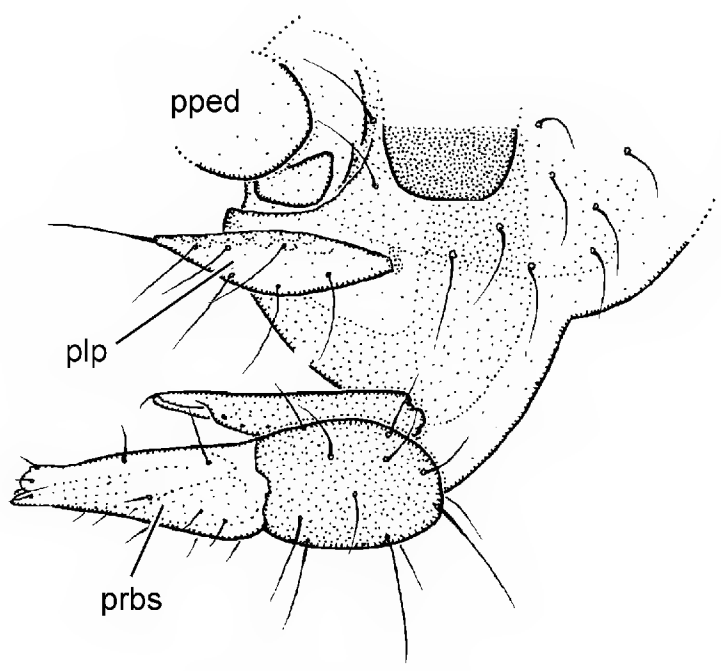
57 *Razorfemora* ♂

Figs 59.46–57. Mouthparts of Phoridae: (46) proboscis, palpus and antenna of *Ptochomyia cummingae* Disney, left lateral view ♀; (47) palpus of *Aenigmatopoeus kohli* Schmitz, ventral view ♀; (48) same, *Cheiloxenia obesa* Delachambre ♀; (49) distiproboscis of *Dohrniphora cornuta* (Bigot *in* de la Sagra), dorsal view ♀; (50) labrum of *Gymnoptera simplex* (Brues), dorsal view ♀; (51) palpus of *Haulepta sheasbyi* Disney, ventral view ♂; (52) same, *Hypocerides nearcticus* Borgmeier ♂; (53) same, *Miclepta arrujumensis* Disney ♀; (54) same, *Microselia yemenensis* Disney ♀; (55) proboscis and palpus of *Necperissa tinglei* (Disney), right dorsal view ♀; (56) palpus of *Perittophora couturieri* Disney, left dorsal view ♀; (57) same, *Razorfemora nussbaumi* Disney ♂. Figs 46, 47, 55, 56 (Disney 1994, figs 8.77d, 8.23a, 8.64e, 8.69b, respectively), Fig. 48 (Disney & Kistner 1995, fig. 4), Fig. 49 (Disney & Kistner 1998, fig. 45), Fig. 50 (Disney 2003e, fig. 8), Fig. 51 (Disney & Kistner 1997, fig. 9), Figs 52–54, 57 (Disney 2006, figs 47, 62, 90).

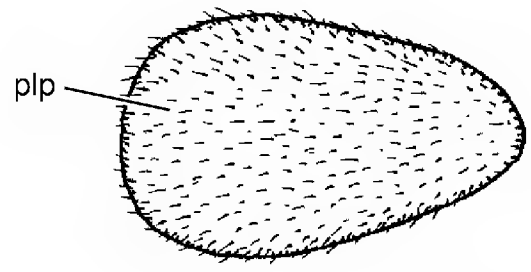
Abbreviations: lbr – labrum; plp – palpus; pped – postpedicel; prbs – proboscis.

(Schmitz, 1955) with *Od. fulleri*, *Od. nolaensis* and *Od. planiceps* Sjöstedt; *T. zimbraunsi* Disney, 1994 with *Od. latericius* and *Od. transvaalensis*; *Termitosagma henningsi* with *Od. badius*, *Od. culturarum* and *Od. patruus* (Sjöstedt); *Termitoscrofa brevis* Delachambre, 1966 with *Megaprotermes giffardii*; *T. pinguissima* Schmitz, 1936 with *Od. badius* and *Od. montanus*; *Termitostroma schmitzi* Reichensperger, 1931 with *Od. badius*, *Od. culturarum* and *Od. patruus*; *Termitoxenia havilandi* Wasmann, 1900 with *Od. latericius*; *T. kistnerorum* Disney, 1995 with *Od. interveniens* Sjöstedt, *Od. lacustris* and *Od. latericius*; and *T. oligoseta* (Disney, 1990) with *Od. lacustris*.

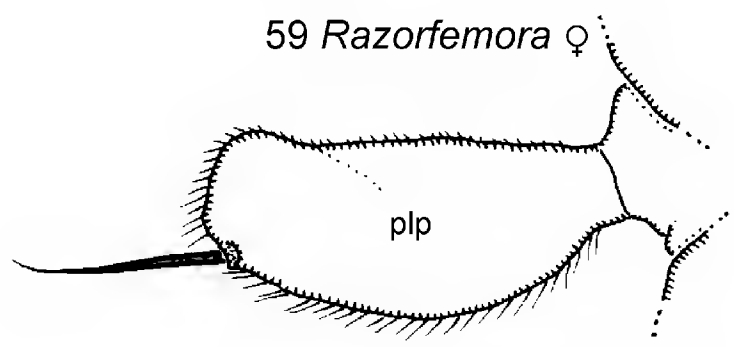
Other termitophiles include: *Dohrniphora diminuens*, *Do. schmitzi* Kohl, *Dundophora fimbriiterga* Schmitz, 1955,



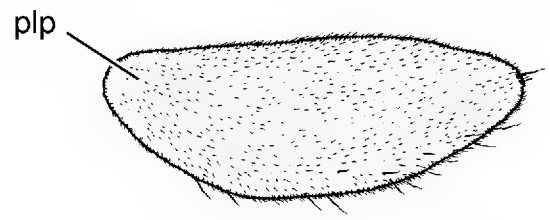
58 *Termitoxenia* ♀



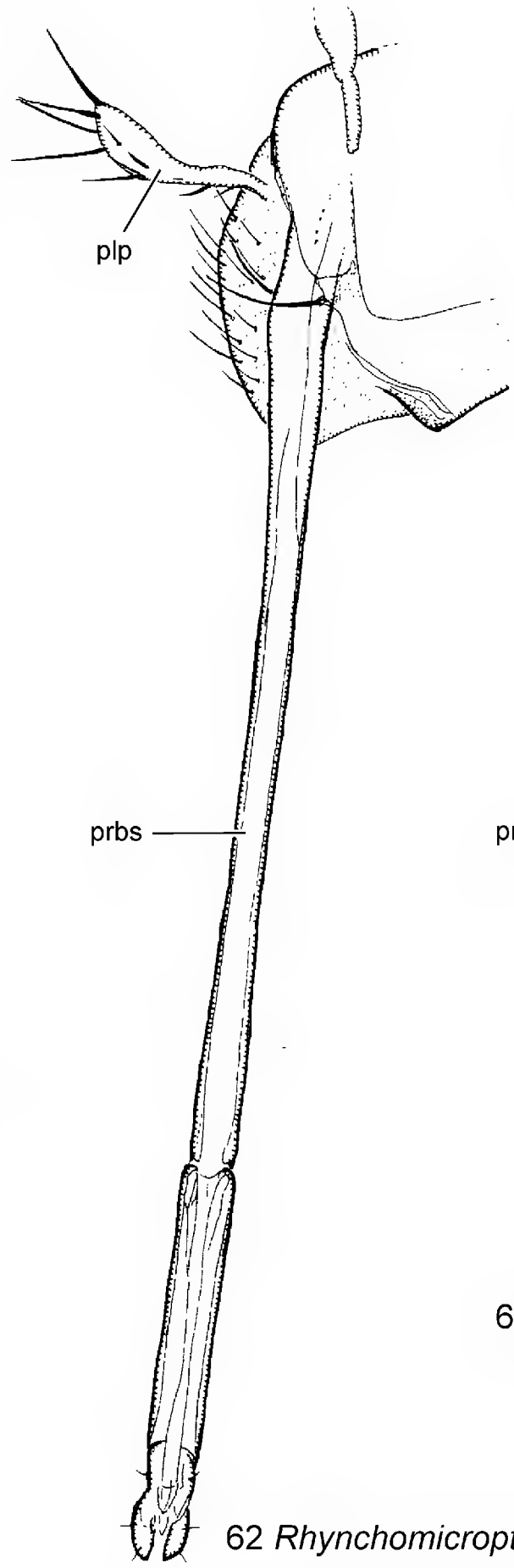
59 *Razorfemora* ♀



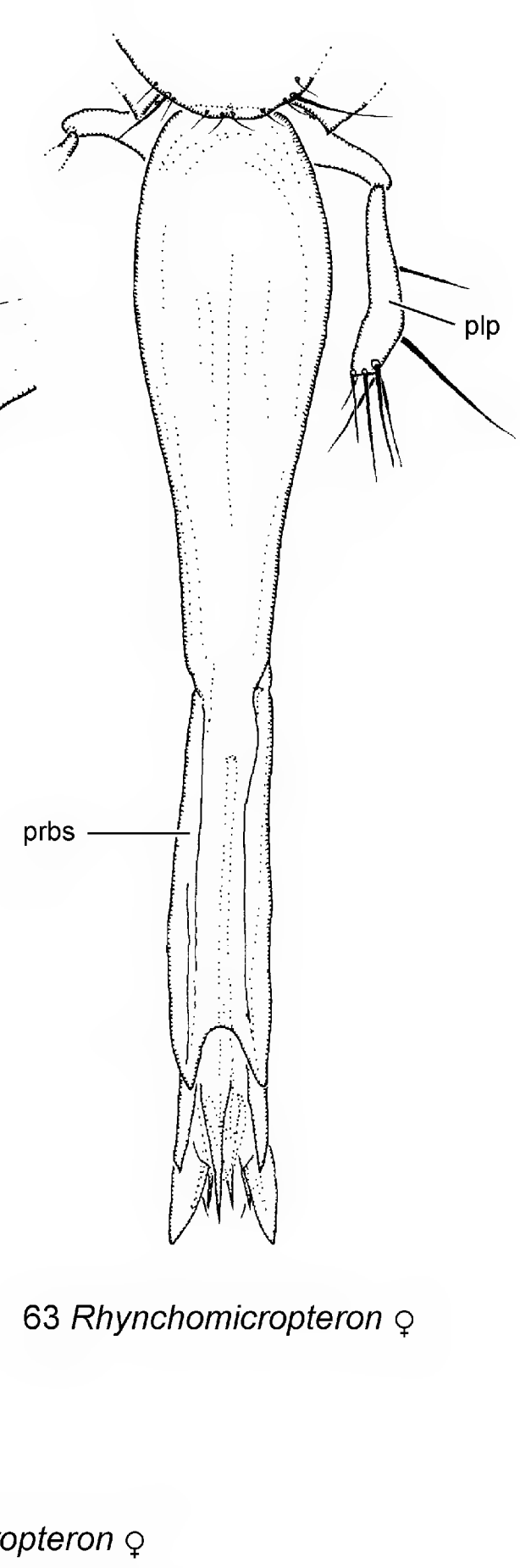
60 *Thaumatoxena* ♂



61 *Woodiphora* ♂



62 *Rhynchomicropteron* ♀



63 *Rhynchomicropteron* ♀

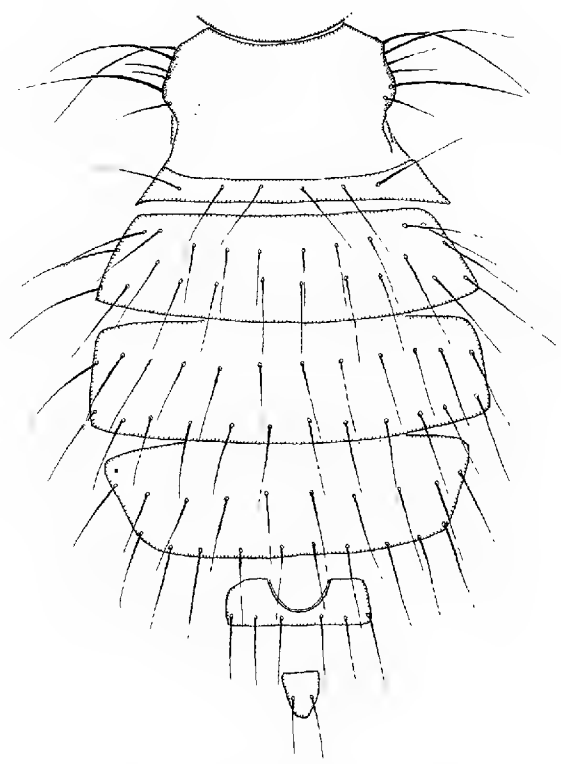
Figs 59.58–63. Mouthparts of Phoridae: (58) proboscis and palpus of *Termitoxenia parvicaliculorum* Disney, left lateral view ♀; (59) palpus of *Razorfemora nussbaumi* Disney, lateral view ♀; (60) same, *Thaumatoxena andreinii* Silvestri ♂; (61) same, *Woodiphora afrotropica* Disney ♂; (62) palpus and proboscis of *Rhynchomicropteron* sp., dorsal view (non-Afrotropical) ♀; (63) same, dorsal view. Fig. 58 (Disney & Kistner 1995, fig. 149), Figs 59, 61 (Disney 2006, figs 91, 122), Fig. 60 (Disney 1994, fig. 8.89b), Figs 62, 63 (Disney & Kistner 1998, figs 69, 70).

Abbreviations: plp – palpus; pped – postpedicel; prbs – proboscis.

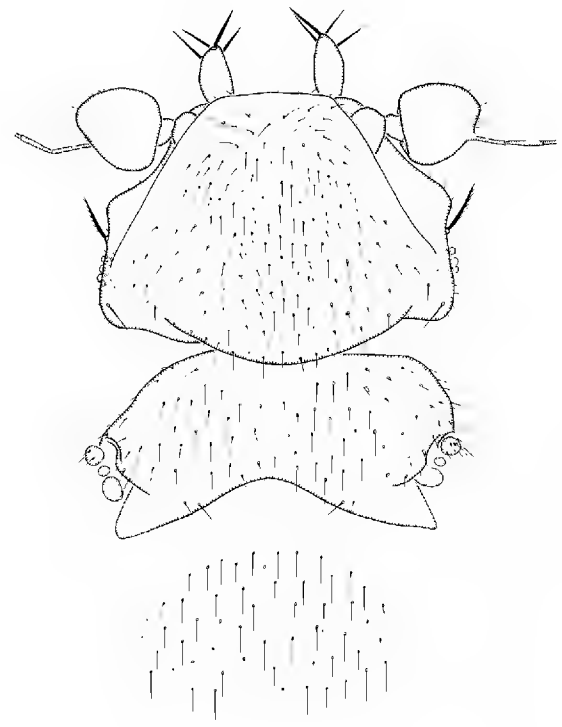
Metopina obsoleta Beyer, 1960, *Puliciphora clover* (Disney, 1989), *Pu. decachete* Schmitz, 1958, *Pu. etiamodesta* Disney, 2005, *Pu. hirta* (Schmitz, 1951), *Pu. sulcimanae* Disney, 1989 and *Thaumatoxena* Breddin & Börner species (Disney & Darlington 1998, 2000*b*; Disney & Kistner 1989, 1992).

Among the common parasitoids of larval and puparial Phoridae are Hymenoptera, especially the family Braconidae. Adults are frequently parasitised by nematodes. *Megaselia halterata* (Wood, 1910) is, for example, parasitised by *Howardula husseyi* Richardson, the lifecycle of which was described by Richardson *et al*. (1977). An adult male of *M. curtinoides* Disney, 1991 was recorded with a planidium-type larva (Hymenoptera) in the abdomen (Disney 1979*b*, 1991*b*). The anomorph states (hyphal bodies) of the fungus *Cordyceps*, or a related genus, were recorded in *Megaselia microcurtineura*, *Syntermitoxenia jaegerskioeldi* and *Termitoxenia oligoseta* (Disney 1991*a*).

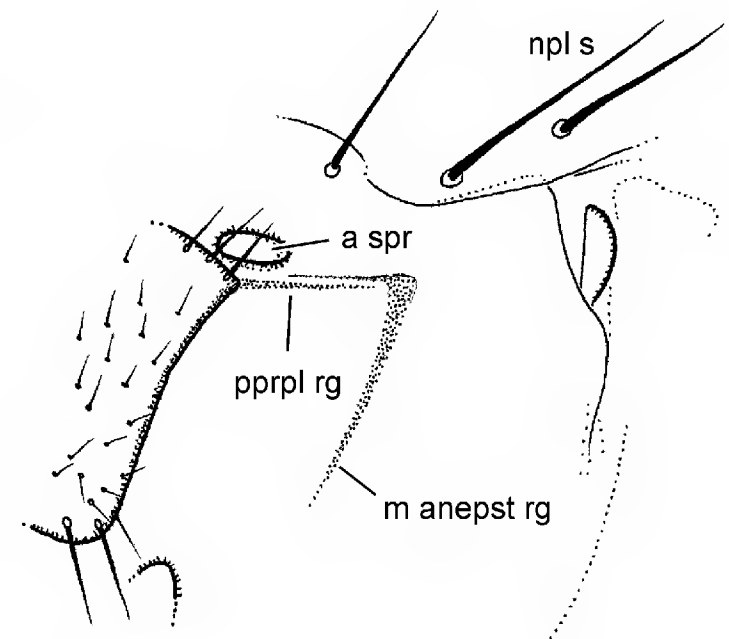
The scuttle fly fauna of the continental Afrotropics remains poorly documented and certain habitats or parts thereof remain almost unexplored. For example, pioneering collections



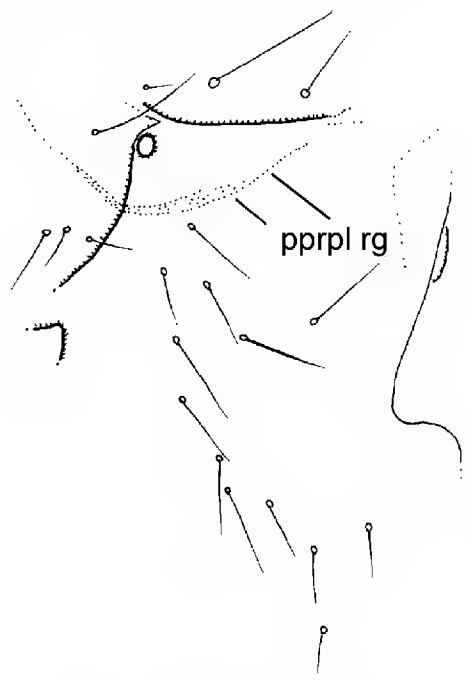
64 *Aenictacantha* ♀



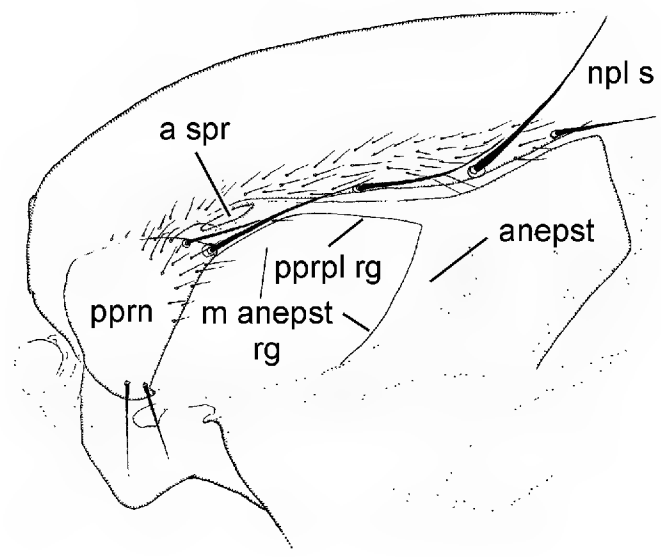
65 *Rhynchomicropteron* ♀



66 *Megaselia* ♀



67 *Perittophora* ♀



68 *Phalacrotophora* ♂

69 *Ptochomyia* ♀

Figs 59.64–69. Head and thorax and thoracic features of Phoridae: (64) thorax and abdomen of *Aenictacantha setifera* Disney, dorsal view ♀; (65) head, thorax and part of abdomen of *Rhynchomicropteron* sp., dorsal view (non-Afrotropical) ♀; (66) detail of thorax of *Megaselia scalaris* Loew, left lateral aspect ♀; (67) female mesopleuron of *Perittophora couturieri* Disney, lateral view ♀; (68) same, *Phalacrotophora* sp., left lateral view ♂; (69) same, *Ptochomyia cummingae* Disney ♀. Fig. 64 (Disney & Kistner 1998, fig. 60), Fig. 65 (Disney 1992, fig. 1), Fig. 66 (Disney 2008*b*, fig. 95), Fig. 67 (Disney & Kistner 1995, fig. 26), Fig. 68 (Disney 2006, fig. 127, as *Zygtaxphora*), Fig. 69 (Disney 1994, fig. 8.77c).

Abbreviations: a spr – anterior spiracle; anepst – anepisternum; m anepst rg – mid anepisternal ridge; npl s – notopleural seta; pprn – postpronotum; pprpl rg – postpropleural ridge.

from the canopies of trees yielded previously unknown species (Disney 1982*b*) and Srivathsan *et al*. (2019), estimated 200,000 species of Afrotropical Phoridae, based on a barcoding study conducted in Uganda.

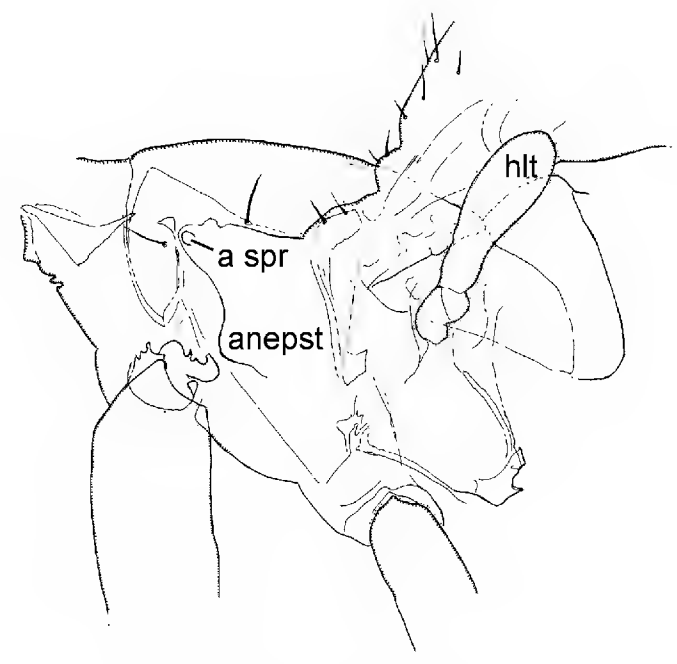
Economic significance

The introduced species *Megaselia halterata* and *M. sandhui* Disney, 1981, which are abundant in the Southern Arabian Peninsula, are serious pests of cultivated agaric mushrooms, such as *Agaricus bisporus* (J.E. Lange) Imbach (Disney 1981*b*). Control measures are discussed by Sandhu & Arora (1990) and White (1985). The widespread *M. curtineura* and *M. scalaris* breed in a range of organic materials and are liable to contaminate human foods, with a consequent risk of introducing pathogenic micro-organisms. Following the successful infection of *M. halterata* with the nematodes *Heterorhabditis heliothidis* (Khan, Brooks & Hirschmann) (Heterorhabditidae) and *Steinernema feltiae* (Filipjev) (Steinernematidae), in the laboratory (Richardson & Chanter 1979; Rinker & Snetsinger 1984; Scheepmaker *et al*. 1995), Erier *et al*. (2009) reported on the subsequent use of *S. feltiae* in the control of this fly, as well as the use of the bacterium *Bacillus thuringiensis israelensis* Barjak (Bacillaceae). A species of *Megaselia* in Hawaiian Is. is attracted to the semiochemical of an introduced fruit fly pest employed in its control (Asquith & Kido 1994). This suggests that the pheromones of pest species of phorid might potentially be used in the same way.

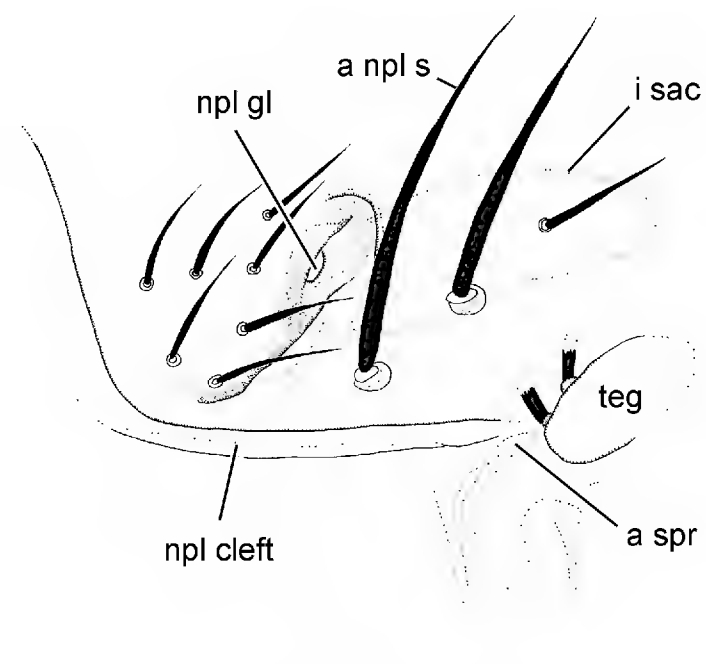
Classification

There is general consensus that the family Phoridae is monophyletic and is placed in the suborder Brachycera, division Cyclorrhapha (= Muscomorpha of some authors), in the superfamily Platypezoidea, which comprises the five families Lonchopteridae, Phoridae and Platypezidae and the two non-Afrotropical families Ironomyiidae and Opetiidae (Brown *et al*. 2015; Cook *et al*. 2004; Lambkin *et al*. 2012; Young 2018). A curiosity is the genus *Aenigmatistes*, which has evolved a ptilinum-like fissure independently of the Schizophora, but which in the mature adult remains exposed, rather than being withdrawn into the head or contracted (Disney 1991*d*).

The supra-generic classification of the Phoridae is far from resolved, however. Part of the problem remains that a large number of genera are only known from a single sex and in several cases when the "missing" sex is recognised, it is found to have been assigned to a different subfamily. In the case of the "Termitoxeniinae" and "Thaumatoxeninae", females were long assigned to separate families. The traditional divisions into subfamilies and tribes is exemplified by Borgmeier (1968), with six subfamilies (Aenigmatiinae, Alamirinae, Metopininae, Phorinae, Termitoxeniinae and Thaumatoxeninae) and the Metopininae (with more than half the species in the family), divided into the two tribes: Beckerinini and Metopiniini. The tribe Metopinini was subsequently divided into the Metopinini and Megaseliini, with the latter accommodating those genera with females that possess a Dufour's crop mechanism (at least in their groundplans) (e.g., Fig. 22) (Disney 1989*b*). The traditional scheme was challenged, especially with regard to the subdivision and re-assignment of genera in the Aenigmatiinae and Phorinae, by Brown (1992), on the basis of a number of interesting hypotheses regarding possible synapomorphies. On the basis of these, Brown erected the subfamilies Conicerinae and Hypocerinae for former sections of the Phorinae and moved some genera into the Aenigmatiinae, which he subdivided into the tribes Aenigmatiini and Diplonevrini. To date, the two most comprehensive, higher-level phylogenetic studies within the family are Ament (2017) and Brown *et al*. (2015), although both



70 *Syntermitoxenia* ♀



71 *Woodiphora* ♂

Figs 59.70–71. Thoracic features of Phoridae: (70) thorax of *Syntermitoxenia kensmithi* (Disney), left lateral view ♀; (71) notopleuron of *Woodiphora afrotropica* Disney, left lateral view ♂. Fig. 70 (Disney 1979a, fig. 4), Fig. 71 (Disney 1994, fig. 8.93c).

Abbreviations: a npl s – anterior notopleural seta; a spr – anterior spiracle; anepst – anepisternum; hlt – halter; i sac – internal sac; npl cleft – notopleural cleft; npl gl – notopleural gland; teg – tegula.

of these studies focus primarily on relationships within the subfamily Phorinae.

Subsequent linking of the sexes for species in genera exhibiting marked sexually dimorphism continues to modify generic assignments. Procurement of mating pairs of the former subfamily Alamirinae, for example, revealed that this subfamily was merely comprised of young, flying stage, females of the "Termitoxeniinae" and that males had been assigned to the Metopininae in error (Disney & Cumming 1992). Likewise, males and females of *Psyllomyia* had not only been assigned to separate genera, but to different tribes of Aenigmatiinae, prior to being correctly associated (Brown 1994). Some of Brown's proposed synapomorphies were called into question (e.g., Disney 1994: 296, 2003*a*). Consideration of the location of the dorsal abdominal glands in females of Metopininae gave rise to the abolition of the Beckerinini and Megaseliini, which were incorporated into the resurrected tribe Gymnophorini (Disney 2003*d*). These data also served to transfer *Aenigmatopoeus* from the Aenigmatiini to the Metopinini. The main problems remain with regard to the subordinate groups within the Phorinae. More recently, Brown *et al*. (2015) provided a mass of new morphological data, especially with regard to the thorax and revised some of Brown's (1992) proposals, especially with regard to the subdivision of the Phorinae into tribes. They returned the non-Afrotropical genus *Triphleba* Rondani to the Phorinae on the basis of new morphological evidence, although molecular evidence had already shown this to be so (Smith & Brown 2008). Otherwise, they did not refer to the evidence from molecular data briefly reviewed below.

The above brief review sketches the state of things before the advent of molecular analyses. These data indicated the affinities of the "Termitoxeniinae" to be with the genera *Diplonevra* Lioy, *Dohrniphora* and *Thaumatoxena* (Cook *et al*. 2004), whereas Brown *et al*. (2015) retained the "Termitoxeniinae" as a separate subfamily. Cook *et al*. (2004) linked *Chonocephalus* with *Metopina* Macquart, but with the former strongly divergent. Brown *et al*. (2015), however, placed *Chonocephalus* in Chonocephalinae, between Sciadocerinae and the remainder of the Phoridae. In this case, the morphology has probably provided a better indication of affinity than the molecular data. Zhao *et al*. (2010) re-assigned several genera between Brown's "Hypocerinae" and "Conicerinae". For example, they grouped *Stichillus* Enderlein with *Diplonevra* and *Dohrniphora*, by contrast with it being grouped with *Borophaga* Enderlein. Brown *et al*. (2015) were correct to leave the subgroups within the Phorinae unresolved, given our current state of knowledge. Clearly, further revisions of the current classification(s) are to be expected. The algorithms employed for generating cladograms tend to downplay the overwhelming evidence (e.g., Moore & Willmer 1997), for the prevalence of convergent evolution. Furthermore, the greater degree of linkage between the character states employed, the more will procedures based primarily on congruence and/or probability amount to circular arguments. Several genera are likely to be re-classified in the future, as the subfamilies and tribes are better characterised, in terms of the phylogenetic reconstruction of the family. For the purposes of reference, the following tentative classification of the Phoridae is suggested: Chonocephalinae, Metopininae (with two tribes: Gymnophorini and Metopinini), Phorinae and Sciadocerinae.

It is to be hoped, that future research will result in a consensus with regard to a phylogenetic classification of genera. By contrast, categorisation (the assignment of a rank to each component clade), owes more to historical accident than scientific insight. Its guiding principle, therefore, is to minimise the changes to the ranks assigned in the past in order to reduce confusion.

The relict Cretaceous subfamily Sciadocerinae is now restricted to Australia, New Zealand and South America. While the genus *Aenigmatistes* is currently assigned to the Phorinae, in reality, it stands on its own, as it is reportedly the only genus of "Aschiza" to have independently evolved a ptilinum-like fissure, which remains exposed in the adult (Disney 1991*d*). The dorsoventral flattening of the females is likely to prove to be due to convergence, rather than a synapomorphy.

Identification

It must be emphasised, that the Phoridae fauna of the Afrotropical Region is still very poorly documented; some genera may not yet be recorded from the region and numerous species remain undescribed, some of which may be atypical. For these reasons, the following identification key may not lead to an identification in all cases. The key is based on specimens initially preserved in alcohol and subsequently mounted on slides, which are examined with a compound microscope. For the writers' preferred method of slide-mounting the reader is referred to Disney (2001).

Key to genera of Afrotropical Phoridae

1. Males. 2
– Females 66
2. Wings absent 3
– Wings present, but sometimes reduced in size 4
3. Compound eye with > 40 ommatidia . . . . . *Aptinandria* Schmitz
– Compound eye with < 15 ommatidia . . . . . *Arrenaptenus* Schmitz
4. Wing with 2, or usually more, setulae on upper surface of vein R_1 and none to as many, but much smaller, setulae on radial sector (*Rs*) and sometimes a setula on vein R_{2+3}; mid tibia with pair of near-dorsal setae in basal ¼ and anteroventral row of small setae in basal ⅔; thorax with anepisternum setulose;

scutellum with 4 marginal setae and variable number of setulae interspersed; terminalia with hypopygium as illustrated in Figs 196, 197 . . . . . *Phlebothrix* Borgmeier

– Without above combination of characters 5

5. Wing with radial sector (*Rs*) (*i.e.*, vein R_{4+5} before apical fork), with several setulae along dorsal surface (*e.g.*, Figs 114, 115), which may be short and fine (or at least shorter and finer than more hair-like seta at base of vein) 6

– Wing with *Rs* bare along dorsal surface, aside from microtrichia and a few setulae (usually only 1) in basal ¼ 9

6. Hind tibia with at least 1 dorsal, or near-dorsal, longitudinal setal palisade (as in Figs 168, 171) 7

– Hind tibia without dorsal setal palisade, but may be spaced setulae (as in Figs 133, 144) 8

7. Head with posterior ocelli well-removed from eye margin; ocellar triangle not demarcated at front by sinuous furrow . . . . . *Borophaga* Enderlein

– Head with posterior ocelli close to eye margin; ocellar triangle strongly demarcated at front by sinuous furrow (Fig. 21) . . . . . *Stichillus* Enderlein

8. Costal wing vein (C) *ca* ⅖ wing length; head with upper interfrontal setae . . . . . *Brachyselia* Schmitz

– Costal wing vein (C) < ⅖ wing length (Fig. 76); head without upper interfrontal setae; terminalia with hypopygium as illustrated in Fig. 186 . . . . . *Euryphora* Schmitz

9. Antennal postpedicel with apex drawn-out into long, narrow, long-setulose process; with longer, short-pubescent arista inserted near base of apical process . . . . . *Diplostylocera* Borgmeier

– Antennal postpedicel and arista not as described above (*e.g.*, Figs 23, 26) 10

10. Antennal postpedicel with apex drawn-out into long, tapered extension, bearing apical arista (*e.g.*, Figs 23, 26) 11

– Antennal postpedicel with apex not drawn-out in this way (*e.g.*, Figs 6, 7), except in some cases where arista is preapical in position or absent, sometimes arista replaced by apical pseudoarista (an extension of postpedicel itself, not articulating with it) 14

11. Mid tibia with 2 differentiated dorsal or near-dorsal setae in basal ½ (*e.g.*, Fig. 142) 12

– Mid tibia without such setae, although row of posterodorsal differentiated setulae may be present along length of tibia 13

12. Hind tibia with isolated setae, including at least 1 pair (1 dorsal and 1 anterodorsal) in basal ½ and lower anterodorsal seta inserted beyond middle (Fig. 142); subcostal wing vein (*Sc*) not reaching vein R_1; antenna as illustrated in Fig. 26; terminalia with surstyli as illustrated in Fig. 177 . . . . . *Conicera* Meigen [in part]

– Hind tibia with only 1 seta in basal ½; antenna not as illustrated above; terminalia with epandrium with at least 1 strong spine at posterolateral extremity of left side (Fig. 187) . . . . . *Gymnoptera* Lioy [in part]

13. Antennal postpedicel as illustrated in Fig. 23; wing vein R_{2+3} absent; anal lobe well-developed (Fig. 73); hind femur slender (Fig. 150); terminalia with anal tube (cercus and hypoproct combined) relatively long (Fig. 176) . . . . . *Arabiphora* Disney

– Without above combination of characters; wing vein M_4 deflected anteriorly in middle section, so that space embraced by it and vein M_2 exhibit characteristic "waist" (Fig. 81) . . . *Metopina* Macquart [in part]

14. Head with front part of frons at right angle to top part of frons, the transition being marked by arch-shaped ridge (Figs 6, 7) . . . . . *Aenigmatistes* Shelford

– Head with frons not as described above 15

15. Mid tibia with at least 2 differentiated dorsal or near-dorsal setae in basal ⅔ (*e.g.*, Fig. 142) 16

– Mid tibia with 1 differentiated dorsal or near-dorsal seta or without setae in basal ⅔ (may be longitudinal row of dorsal differentiated setulae) 26

16. Hind tibia with dorsal, longitudinal setal palisade (*e.g.*, Fig. 168), sometimes with 2 or 3 such palisades (*e.g.*, Fig. 168) 17

– Hind tibia without longitudinal setal palisade, but may be row of spaced setulae or series of overlapping transverse combs 21

17. Wing vein R_{2+3} absent (as in Figs 73, 97, 117) 18

– Wing vein R_{2+3} present (*e.g.*, Fig. 72) 19

18. Head with frontal setae strongly developed; terminalia with hypopygium as illustrated in Figs 189, 190; palpus with 4 setae, typically as in Fig. 52; wing vein R_1 tip as in Fig. 117 . . . . . .*Hypocerides* Schmitz

– Head with frontal setae greatly reduced and supra-antennal setae vestigial or absent (Fig. 14); terminalia with hypopygium relatively short, but high (Figs 211–213); palpus with 1 seta, typically as illustrated in Fig. 60; wing vein R_1 tip as in Fig. 97 . . . . . .*Thaumatoxena* Breddin & Börner

19. Thorax with anepisternum with setulae in upper part; wing with alular ridge with single, generally pale, seta which is broadest in middle; terminalia with hypopygium characterised by short, but high epandrium and non-setulose sclerotised ring at base of anal tube (cercus and hypoproct combined) (Fig. 185); hind femur typically with patch of spinules at base of posterior face (Fig. 151), sometimes with sensory pit as well or other modifications; hind coxa with protruding lobe (Fig. 154) . . . . . .*Dohrniphora* Dahl

– Thorax with anepisternum bare, or if with setulae in upper part, then wing with alular ridge with several setae; otherwise, alular ridge with at least 2 setae, which are generally dark brown or black and evenly tapered; terminalia with hypopygium characterised by epandrium generally longer than high, with or without paired surstyli fused to the sides and hypoproct forming setulose cylinder (e.g., Figs 184, 195), or entirely absent; hind coxa not as described above 20

20. Terminalia with hypoproct forming cylinder, bearing setulae (Fig. 184); epandrium rarely with pair of processes (surstyli) projecting ventrally below hypoproct; cerci well-separated from epandrium (Fig. 184); palpus 2-segmented; hind femora with bases often with spinules and/or processes [NB: in some males with very long anal tubes, cerci poorly differentiated from hypoproct] . . . . . .*Diplonevra* Lioy

– Terminalia with hypoproct not expanded dorsally forming cylinder; cerci with elongated bases positioned immediately behind rear margin of epandrium (Fig. 195); palpus 1-segmented; hind femora not as described above . . . . . *Phalacrotophora* Enderlein [in part]

21. Wing alular ridge with single very long, plumose seta (Fig. 120); costal vein (C) swollen at tip (Fig. 113); terminalia with hypopygium as illustrated in Fig. 179 . . . . . *Beyermyia* Disney

– Wing alular ridge without long, plumose seta, frequently with more than 1 other seta; costal vein and hypopygium not as described above 22

22. Costal wing vein (C) with setae greatly reduced, clearly shorter than width of costal vein . . . . . *Rhynchomicropteron* Annandale

– Costal wing vein (C) with setae normal, longer than width of costal vein. 23

23. Thorax with anepisternum setulose 24

– Thorax with anepisternum bare 25

24. Hind tibia at most with 2 setae in upper ⅔; wing with costal vein (C) extending at most only ⅖ wing length; terminalia with hypopygium not as illustrated below. . . . . .*Mannheimsia* Beyer

– Hind tibia with at least 3 setae in upper ⅔; wing with costal vein (C) extending to at least ⅖ wing length; terminalia with hypopygium as illustrated in Fig. 198 . . . . . *Plethysmochaeta* Schmitz

25. Hind tibia with most basal anterior seta paired with dorsal seta (Fig. 165); terminalia with surstyli in form of distinctive pair of claspers (Fig. 177); epandrium not as described below; head without supra-antennal setae and anterolateral setae, with only 6 setae in front of anterior ocellus; antennal arista inserted apically (Fig. 26) . . . . . *Conicera* Meigen [in part]

– Hind tibia without dorsal seta adjacent to basal anterior seta; terminalia without surstyli; epandrium with at least 1 strong spine at posterolateral extremity of left side (Fig. 187); head with supra-antennal setae; antennal arista not as described above . . . . . *Gymnoptera* Lioy [in part]

26. Hind tibia with 1 or more longitudinal rows of palisades setae (Fig. 156); mid tibia with 1 differentiated seta in basal ½; scutellum with only 4 setulae or setae; terminalia with hypopygium as illustrated in Fig. 199 . . . . . *Psyllomyia* Loew

– Hind tibia at most with 1 longitudinal row of palisade setae; mid tibia without differentiated seta in basal ½, but may be longitudinal row of near-dorsal or dorsal setulae; scutellum with various numbers of setae; terminalia with hypopygium not as described above 27

27. Hind tibia with dorsal, longitudinal row of palisade setae (as in Fig. 168) 28

– Hind tibia without dorsal row of palisade setae (but spaced setulae may be present) 54

28. Thorax with anepisternum setulose, sometimes with 1 or more additional setae, rarely with single strong seta only 29

– Thorax with anepisternum bare 40

29. Wing vein R_{2+3} absent (as in Fig. 73). 30
– Wing vein R_{2+3} present (as in Fig. 72) 35
30. Scutellum with at least 6 setae; head with 6 or more supra-antennal setae, but otherwise without setae on frons between these and anterior ocellus . . . . . *Aenigmatopoeus* Schmitz
– Scutellum with 4 setae, 2 setae and 2 setulae or 2 setae only; head with only 4 supra-antennal setae, but with several strong setae between these and anterior ocellus 31
31. Abdominal venter with paired pigmented patches on segment 5 (Figs 175, 218); male terminalia with hypopygium as illustrated in Fig. 175; antenna as illustrated in Fig. 35; fore tarsus as illustrated in Fig. 138 . . . . . .*Plastophorides* Beyer
– Abdominal venter without pigmented patches; male terminalia with hypopygium, antenna and fore tarsus not as illustrated above. 32
32. Wing veins R_1 and R_{4+5} virtually parallel; head with frons with median furrow vestigial (Fig. 19); palpus globose (Fig. 51); terminalia with terminal setulae of proctiger weak and lobes at rear of hypandrium scarcely developed (Fig. 188). . . . . *Haulepta* Disney
– Wing veins R_1 and R_{4+5} apically divergent (e.g., Fig. 99); head with frons with median furrow well-developed (e.g., Fig. 12); palpus more elongate; terminalia not as described above 33
33. Hind tibia with anterodorsal row of differentiated setulae as well as posterodorsal row (2 rows separated by palisade setae). 34
– Hind tibia without anterodorsal row of differentiated setulae 35
34. Palpal setae or supra-antennal setae, or both, clearly longer than upper occipital setae. . . . . .*Megaselia* Rondani [in part]
– Palpal setae and supra-antennal setae only *ca* size of upper occipital setae, but former sometimes slightly longer . . . . . *Phalacrotophora* Enderlein [in part]
35. Head with frons narrow, height clearly much greater than breadth; wing with costal vein (C) extending *ca* ½ wing length; antennal postpedicel *ca* 2 × as long as broad . . . . . .*Ceratophoromyia* Beyer
– Head with frons not obviously narrowed or with breadth greater than height; costal wing vein (C) and antennal postpedicel not as described above 36
36. Head with 0–2 reduced supra-antennal setae (Fig. 20); scutellum with 4 setae; thorax with 3 notopleural setae; wing with tip of subcostal vein (Sc) confluent with vein R_1; terminalia with hypopygium as illustrated in Fig. 205 . . . . . *Ritchiephora* Disney
– Without above combination of characters 37
37. Terminalia with anal tube (cercus and hypoproct combined) clearly longer than dorsal face of epandrium (e.g., Fig. 192); thorax with anepisternum with long seta posteriorly, as well as setulae 38
– Terminalia with anal tube only slightly, if any, longer than dorsal face of epandrium (e.g., Fig. 215) . . . 39
38. Terminalia with anal tube (cercus and hypoproct combined) not slender and long (Fig. 191) . . . . . .*Megaselia* Rondani [in part]
– Terminalia with anal tube slender, very long relative to length of epandrium (Fig. 192) . . . . . *Menozziola* Schmitz
39. Wing vein R_{2+3} absent (as in Fig. 73). 40
– Wing vein R_{2+3} present (as in Fig. 72) 42
40. Compound eye with lower ommatidia at least 2 × diameter of uppermost ommatidia (Fig. 15); antennal postpedicel longer than greatest breadth; head with strong pair of supra-antennal setae, but each standing in triad with an antial and anterolateral seta, thus much farther apart than pre-ocellar setae (Fig. 15); terminalia with anal tube (cercus and hypoproct combined) long relative to epandrium (Fig. 214); wing as illustrated in Fig. 98 . . . . . .*Veranophora* Disney [in part]
– Without above combination of characters 41
41. Thorax without notopleural cleft (Fig. 66). . . . . .*Megaselia* Rondani [in part]
– Thorax with notopleural cleft (Fig. 71) . . . . . *Woodiphora* Schmitz [in part]
42. Hind tibia with more than 1 dorsal longitudinal row of palisade setae (Fig. 172). . . . . *Woodiphora* Schmitz [in part]
– Hind tibia with 1 dorsal longitudinal row of palisade setae (e.g., Fig. 168) 43

43. Hind femur with triangular projection at base (Fig. 162); antennal postpedicel clearly longer than broad (Fig. 38); terminalia with anal tube (cercus and hypoproct combined) shorter than epandrium (Fig. 204). . . . . *Razorfemora* Disney

– Without above combination of characters 44

44. Hind tibia with clearly differentiated anterodorsal row, as well as a posterodorsal row, of setulae (2 rows separated by palisade setae); palpal setae and supra-antennal setae only *ca* size of upper occipital setae, but former sometimes slightly longer . . . . . *Phalacrotophora* Enderlein [in part]

– Hind tibia with (at most) posterodorsal row of differentiated setulae on dorsal face; palpal setae and supra-antennal setae at least as long as upper pair of supra-antennal setae clearly longer than upper occipital setae 45

45. Antennal postpedicel globose. 46

– Antennal postpedicel longer than its greatest breadth. 47

46. Thorax with anterior end of notopleuron without duct opening of notopleural gland (Fig. 66); terminalia with anal tube (cercus and hypoproct combined) longer than epandrium (Fig. 191) . . . . . *Megaselia* Rondani [in part]

– Thorax with anterior end of notopleuron with duct opening of notopleural gland, concealed (at least in part) within notopleural cleft, with length greater than diameter of anterior thoracic spiracle (Fig. 71); terminalia with anal tube at most only *ca* as long as epandrium (Fig. 215). . . . . *Woodiphora* Schmitz [in part]

47. Terminalia with anal tube (cercus and hypoproct combined) clearly longer than epandrium (NB: the single Afrotropical species probably represents a *Megaselia* with unusually long postpedicel) . . . . . *Macrocerides* Borgmeier

– Terminalia with anal tube (at most), as long as mid-line length of epandrium 48

48. Hind tibia without differentiated row of posterodorsal setulae . . . . . *Megaselia* Rondani [in part]

– Hind tibia with differentiated longitudinal row of posterodorsal setulae 49

49. Costal wing vein (C) extending < ½ length of wing; terminalia with epandrium longer than high, with posterolateral lobes well-developed below anal tube (Fig. 193); antenna as illustrated in Fig. 31 . . . . . .*Microselia* Schmitz

– Costal wing vein (C) extending to middle of wing or beyond; terminalia with epandrium and antenna variable 50

50. Wing with at least 4 setae on alular ridge (as in Fig. 72) 51

– Wing with at most 3 setae on alular ridge. 53

51. Thorax with anepisternum and anterior spiracle distorted (Fig. 68); costal wing vein (C) with > 2 rows of cilia in (at least) basal ½. . . . . *Phalacrotophora* Enderlein [in part]

– Without above combination of characters 52

52. Without below combination of characters . . . . . *Megaselia* Rondani [in part]

– Compound eye with lower ommatidia at least 2 × diameter of uppermost ommatidia (Fig. 15); antennal postpedicel longer than greatest breadth; head with strong pair of supra-antennal setae, but each standing in triad with an antial and anterolateral seta, thus much farther apart than pre-ocellar setae (Fig. 15); terminalia with anal tube (cercus and hypoproct combined) long relative to epandrium (Fig. 214); wing as illustrated in Fig. 98 . . . . . *Veranophora* Disney [in part]

53. Wing vein R_{2+3} present (e.g., Fig. 99) (NB: fork may be so close to wing tip as to appear unforked; dubious cases key both ways). 54

– Wing vein R_{2+3} absent (e.g., Fig. 81). 55

54. Head with frons with median furrow, but setae reduced to fine setulae (Fig. 10); wing as illustrated in Fig. 75; thorax without notopleural gland; flies somewhat dorsoventally flattened . . . . . *Danumphora* Disney [in part]

– Without above combination of characters; thorax with notopleural gland, but this at least partly concealed by notopleural cleft (Fig. 71), the length of latter greater than diameter of anterior thoracic spiracle . . . . . *Woodiphora* Schmitz [in part]

55. Wing with alular ridge with at least 1 seta; subcostal vein (*Sc*) well-developed (Fig. 99); thorax with notopleural cleft (Fig. 71), greater in length than diameter of anterior thoracic spiracle; terminalia with

anal tube (cercus and hypoproct combined) (at most), subequal to length epandrium, usually clearly shorter (Fig. 215) . . . . . *Woodiphora* Schmitz [in part]

– Wing with alular ridge without setae; subcostal vein (*Sc*) absent; thorax without notopleural cleft; terminalia with anal tube variable 56

56. Wings somewhat reduced (Figs 77, 78); head without posterior ocelli; frontal setae absent, apart from 1 reduced pair of supra-antennal setae and 1 pair of ocellar setae . . . . . *Metopina* Macquart [in part]

– Without above combination of characters 57

57. Costal wing vein (*C*) extending at most ⅓ of wing length (e.g., Figs 83, 86, 91, 92, 96); terminalia with anal tube (cercus and hypoproct combined) clearly shorter than epandrium (e.g., Figs 194, 200, 208–210). 58

– Costal wing vein (*C*) extending at least ⅖ wing length (e.g., Figs 86, 91); terminalia with anal tube shorter or longer than epandrium (e.g., Figs 180, 181, 201–203) 62

58. Antennal arista long-pubescent (e.g., Figs 36, 42) 59

– Antennal arista short-pubescent (e.g., Fig. 45) or slightly longer 60

59. Antennal arista with second article broader than long (Fig. 36); wing veins M_1, M_2 and M_4 ending well before wing margin (Fig. 86) . . . . . *Ptochomyia* Silvestri

– Antennal arista with second article longer than broad (Fig. 42); wing veins M_1, M_2 and M_4 ending very close to wing margin (Fig. 91). . . . . *Termitophilomyia* Schmitz

60. Thorax without propleural seta (propleuron bare); fore tarsal segments relatively short (Fig. 130); terminalia with hypopygium as illustrated in Fig. 210 . . . . . *Termitoxenia* Wasmann

– Thorax with at least 1 fine propleural seta in lower ½; fore tarsal segments not shortened; terminalia with hypopygium not as described above (e.g., Figs 194, 209) 61

61. Antennal arista with basal articles distinctly longer than broad (Fig. 33); terminalia with hypopygium as illustrated in Fig. 194; fore leg as illustrated in Fig. 126; wing not as illustrated below. . . . . *Necperissa* Disney

– Antennal arista with basal articles (at most), as long as broad (Fig. 43); terminalia with hypopygium as illustrated in Fig. 209; fore leg not as illustrated above; wing as illustrated in Fig. 92. . . . . *Termitosagma* Reichensperger

62. Ocelli absent; wing with subcostal vein (*Sc*) strongly developed, its tip joining vein R_1 . . . . . *Wandolleckia* Cook

– Ocelli present; wing with subcostal vein (*Sc*) present or absent. 63

63. Terminalia with anal tube (cercus and hypoproct combined) variable (Figs 201–203), if slightly shorter, then cerci distinctly longer than high (Figs 202, 203); wing with subcostal vein (*Sc*) strongly developed, its tip fused with vein R_1 (Fig. 87) . . . . . *Puliciphora* Dahl

– Terminalia with anal tube distinctly shorter than epandrium; cerci slightly, if any, longer than high (e.g., Fig. 182); wing with subcostal vein (*Sc*) present or absent. 64

64. Wing veins M_2 and M_4 virtually straight, or only slightly sinuous, so no obvious constriction of space between the two veins (Fig. 74); vein M_1 with at least basal ¼ absent (Fig. 74); terminalia with hypopygium compact, often complex (Figs 180–182). . . . . *Chonocephalus* Wandolleck

– Wing veins M_4 deflected forwards in middle ⅓, or just beyond, so space between veins M_2 and M_4 slightly to very markedly constricted (Fig. 81); vein M_1 with basal ¼ well-developed (Fig. 81); terminalia with hypopygium not as described above. 65

65. Wing vein M_4 strongly deflected and anal lobe (*i*.e., part of wing bearing vein *CuA*+*CuP*) (Fig. 81) with inner border at relatively steep angle to alular ridge (Fig. 81) . . . . . *Metopina* Macquart [in part]

– Wing vein M_4 less strongly deflected. . . . . *Penthaplus* Schmitz

66. Wings and halteres entirely absent (e.g., Figs 3, 64); wing rudiments sometimes fused to thorax and not articulated with it (NB: in some cases, wing rudiments may be partly fused to thorax and sometimes development of anterior abdominal segments may conceal wing stumps, in such cases genera key both ways; if halteres are present proceed to couplet 82). 67

– Wings developed, but may be reduced (e.g., Figs 103–112), or reduced to rudiments or stumps (e.g., Figs 4, 65, 100–102); halteres usually present. 82

67. Terminal abdominal segments directed rearwards 68

– Terminal abdominal segments deflected ventrally, even to extent of anus being directed forwards . . . 92

68. Abdominal tergites entirely absent 69

– At least abdominal tergite 2 present, even if weakly pigmented (NB: variable genera key both ways) 70

69. Mid tibia with pair of setae in basal ½; head with 3 ocelli . . . . . *Diplonevra* Lioy [in part]

– Mid tibia without pair of setae in basal ½, but may be some long setulae along dorsal face; head without ocelli 70

70. Abdomen without tergites 3 and 4, but tergite 2 and sometimes tergite 5 present 71

– Abdomen with tergites 2–5 and sometimes tergites 1 and 6 present 72

71. Abdominal tergite 2 mainly represented by longer setulae, contrasting with other setulae on dorsal surface of abdomen; terminalia without gland complex evident on segment 5 . . . . . *Morahania* Schmitz

– Abdominal tergite 2 > 2 × as wide as long, general setulocity of dorsal surface of abdomen clearly longer than setulae of tarsi . . . . . *Wandolleckia* Cook

72. Shape strongly dorsoventrally flattened (e.g., Fig. 4); head wider than long, with widely separated antennae (e.g., Figs 4, 9) 73

– Shape, head and antennae not as described above 86

73. Hind femur with dorsal, preapical, feathered seta and all tibiae with similar dorsal or near-dorsal setae (Fig. 144); antennae widely separated; head with frons with long setulae (Fig. 5); thorax and abdominal tergites also long-setulose . . . . . *Aenictacantha* Disney

– Without above combination of characters 74

74. Head without supra-antennal setae inserted in middle at front of frons, displaced laterally in association with wide separation of antennae (Fig. 3); other than setae on vertex, which are either reduced or absent, no other setae present on frons; abdomen with 6 tergites extending full width of segments (Fig. 3); terminal abdominal segments as illustrated in Figs 219–221 . . . . . *Chonocephalus* Wandolleck

– Head usually with 2 pairs of supra-antennal setae, inserted in middle at front of frons, antennae usually more closely approximated (may be additional setae on frons, other than supra-antennal setae and those on vertex); abdomen with at most 5 tergites extending full width of segments; terminal abdominal segments not as described above 75

75. Abdominal tergites 1 and 2 tapered laterally, extending well down flanks (Fig. 225) . . . . . *Dundophora* Schmitz

– Abdominal tergites 1 and 2 not tapered as described above 76

76. Ocelli absent 77

– Ocelli present (NB: variable genera key both ways) 79

77. Head with 2 setae on frons between supra-antennal setae and those on vertex . . . . . *Puliciphora* Dahl [in part]

– Head with at least 4 setae on frons between supra-antennal setae and those on vertex 78

78. Abdominal tergites 2–4 each with at most a single transverse row of weaker setae at rear margin only; tergite 5 at most with only small emargination of middle of anterior margin (< ⅓ of tergite width), without semicircular flap . . . . . *Aptinandria* Schmitz

– Abdominal tergites 2–4 each with 2 transverse rows of strong setae (as strong as those on thorax), 1 row in anterior ½ and 1 at rear margin; tergite 5 with large semicircular flap occupying wide emargination of anterior margin (similar to Fig. 231) (if neither option applies proceed to couplet 79) . . . . . *Hexacantherophora* Schmitz

79. Head with frons without setae between supra-antennal setae and those on vertex; abdominal tergite 5 without gland complex in middle of anterior margin 80

– Head with frons with at least 2 setae between supra-antennal setae and those on vertex; abdominal tergite 5 with semicircular flap in middle of anterior margin (e.g., Figs 230, 231) 81

80. Thorax (dorsum) with 6 strong setae near rear margin and single pair in middle ⅓ . . . . . *Penthaplus* Schmitz

– Thorax (dorsum) with 4 strong setae near rear margin, none in middle ⅓ . . . *Puliciphora* Dahl [in part]

81. Compound eyes greatly reduced, their greatest diameter < ½ that of antennal postpedicel . . . . . *Arrenaptenus* Schmitz

– Compound eyes with greatest diameter clearly > ½ that of antennal postpedicel. . . . . .*Puliciphora* Dahl [in part]

82. Wings with at least membranous area (part bearing thin veins) reduced (e.g., Fig. 90), or represented by rudiments only (NB: borderline cases, where membranous area is only reduced slightly key out both ways) 83

– Wings fully developed (e.g., Fig. 72). 91

83. Wings represented by intact, but reduced wings or by rudiments (e.g., Figs 77–80, 93, 94) 84

– Wings represented by stumps (membranous area having been largely shed, leaving ragged outer margin, or wing missing entirely) (e.g., Figs 100–112) 92

84. Wing rudimentary, with membrane (*i*.e., beyond end of costal vein (C) and behind vein R_{4+5}), greatly reduced or absent, if some of membrane present, then costal index (length of costal vein divided by length of wing) > 0.9. 85

– Wing complete, even if membrane shorter than normal, costal index invariably < 0.9 (e.g., Fig. 86). . . . 91

85. Body strongly dorsoventrally flattened and abdominal segments 1–6 largely covered by single large tergite; antennae in pits; head very much broader than long (Fig. 4), with proboscis shorter than head; hind femur with at least 1 (usually 2) preapical anterior spines (Fig. 163); mid tibia as illustrated in Fig. 143 . . . . . .*Thaumatoxena* Breddin & Börner

– If body strongly dorsoventrally flattened, then abdominal tergites 1–6 largely covered by 6 separate tergites, or tergites 3–6 reduced, so that much of dorsal face membranous; antennae usually clearly not in pits; head, hind femur and mid tibia not as described or illustrated above 86

86. Abdomen with 6 tergites evident, entirely covering dorsal face of abdomen; head with frons with anterior face at right angle to posterior face (Figs 6, 7), sometimes latter greatly shortened (Fig. 9); wing rudiments simple (Figs 100–102) . . . . . *Aenigmatistes* Shelford

– Without above combination of characters 87

87. Without wing rudiments or these fused to posterolateral corners of thorax and not articulated with it; palpus flattened (Fig. 47); hind femur as illustrated in Fig. 149 and hind tibia in Fig. 164; mid tibia with anteroventral row of setae in outer ½ weaker, not darker than adjacent setulae . . . . . *Aenigmatopoeus* Schmitz

– With wing rudiments present, articulating with thorax; palpus and legs not as described above. 88

88. Proboscis clearly longer than head; ocelli absent (e.g., Fig. 13) 89

– Proboscis only marginally longer than head (if at all); ocelli usually present. 90

89. Wing rudiment as illustrated in Fig. 104; head as illustrated in Fig. 13; hind femur and tibia as illustrated in Figs 157, 171; proboscis not as illustrated below . . . . . *Psyllomyia* Loew

– Wing rudiment not as illustrated above, tapering towards tip (Figs 110–112); head and thorax as in Fig. 65; hind femur and tibia simple; proboscis as in Figs 62, 63. . . . . *Rhynchomicropteron* Annandale

90. Thorax much broader than long; wing rudiment simple, with long terminal seta; abdominal tergites 1–5 all broader than long, extending full widths of segments (e.g., tergites 4–6 as in Figs 231, 232); terminalia with cerci normally developed. . . . . .*Puliciphora* Dahl [in part]

– Without above combination of characters 91

91. Wing with 2 thin veins (M_1 and M_4) (e.g., Fig. 84). 92

– Wing with at least 3 thin veins (M_1, M_2 and M_4) (e.g., Fig. 83). 109

92. Fore femur convexly bowed (Fig. 123); palpus as illustrated in Fig. 48 . . . . . *Cheiloxenia* Delachambre

– Fore femur and palpus not as described or illustrated above. 93

93. Costal vein (C) greatly overreaching tip of vein R_{4+5} (Fig. 94), with irregular transverse banding at high magnification (Fig. 119); antennal arista with article 3 long-pubescent (Fig. 44); abdominal segment 7 with venter with posteromedian process bearing setae (Fig. 250) . . . . . *Termitoscrofa* Schmitz

– Without above combination of characters 94

94. Costal vein (C) greatly overreaching tip of vein R_{4+5}, with apical portion demarcated and/or bearing closely crowded costal cilia (e.g., Figs 90, 95, 118). 95

– Costal vein (C) not as described above 97

95. Antennal arista with pubescence on article 3 short; wing as illustrated in Figs 95, 118 . . . . . .*Termitostroma* Reichensperger

– Antennal arista with pubescence on article 3 very long (e.g., Figs 40, 41); wing as illustrated in Fig. 90 96

96. Thorax with notopleuron clothed in microtrichia, with 2 notopleural setae. . . . *Termitomyia* Wasmann

– Thorax with notopleuron devoid of microtrichia, usually with 1 notopleural seta . . . . . *Termitophilomyia* Schmitz [in part]

97. Antennal arista with long, markedly pubescence on article 3 (e.g., Figs 37, 42). 98

– Antennal arista with short pubescence on article 3 (e.g., Fig. 43) 99

98. Palpus longer than abbreviated basiproboscis (Fig. 46) . . . . . *Ptochomyia* Silvestri

– Palpus (at most) as long as basiproboscis. . . . . *Termitophilomyia* Schmitz [in part]

99. Costal wing vein (C) with tip as illustrated in Fig. 103; fore femur grossly inflated (Fig. 124) . . . . . *Linklloydia* Disney

– Costal wing vein (C) and fore femur not as above. 100

100. Basiproboscis only *ca* as long as broad or shorter; labella short, not gradually tapering to pointed tips 101

– Basiproboscis typically markedly longer than broad; labella gradually tapering to pointed tips 104

101. Thorax with anepisternum finely setulose (e.g., Fig. 67) 102

– Thorax with anepisternum bare (e.g., Fig. 70). 104

102. Thorax with propleuron with at least 2 fine setae (e.g., Fig. 67) 103

– Thorax with propleuron bare (e.g., Fig. 70) 104

103. Palpus long, club-like (Fig. 56); thorax with scutum and anepisternum with more numerous setae, anepisternum with long post-propleural ridge (Fig. 67); wing with 2 thin veins (Fig. 85); fore leg as illustrated in Fig. 127 . . . . . *Perittophora* Disney

– Palpus relatively short, leaf-like; thorax with scutum and anepisternum with relatively few setae, anepisternum without post-propleural ridge; wing with 3 thin veins (Fig. 93); fore leg not as illustrated above . . . . . *Termitosagma* Reichensperger

104. Solutrichomes (specialised setae with basal sockets surrounded by small perforations) of anterior abdominal segments, with well-defined fields of closely crowded perforations, but without bounding palisades of erect processes; proboscis, palpus and antenna as illustrated in Fig. 17, but proboscis sometimes more elongated; wing stump as illustrated in Fig. 106. . . . . *Syntermitoxenia* Schmitz

– Solutrichomes either with bounding palisades of erect processes, or with ill-defined fields of perforations; proboscis, palpus and antenna and wing stump not as illustrated above 105

105. Abdominal setae all seemingly with simple sockets (under stereoscan microscopy some may appear surrounded by field of perforations) 106

– Some abdominal setae fully developed solutrichomes (*i.e.*, arising from sockets surrounded by perforated saucer-like discs, with rims made up of series of outwardly projecting lobes, appearing as circle of dashes with the naked eye) 107

106. Thorax with propleuron with at least 1 fine seta; notopleuron with microtrichia; fore tarsus as illustrated in Fig. 135; terminalia with cerci clearly differentiated (Fig. 244) . . . . . *Paratermitoxenia* Beyer

– Thorax with propleuron bare; notopleuron, fore tarsus and cerci not as described or illustrated above 107

107. Palpus rounded apically; basiproboscis elongated (Fig. 55); antenna as illustrated in Fig. 32; halter < 0.03 mm long; fore leg as illustrated in Fig. 126. . . . . *Necperissa* Disney

– Palpus more leaf-like, tapering to point (viewed in profile); basiproboscis less elongate; antenna, wing, halter and fore leg not as described or illustrated above 108

108. Thorax with propleuron bare . . . . . *Termitoxenia* Wasmann

– Thorax with propleuron with at least 1 fine seta in lower $\frac{1}{2}$ 109

109. Wing with 2, or usually more, setulae on upper surface of vein R_1 and none to as many, but much smaller setulae on radial sector (*Rs*) and sometimes setula on vein R_{2+3}; mid tibia with pair of near-dorsal setae in basal $\frac{1}{4}$; hind tibia (Fig. 170) with anteroventral row of small setae in basal $\frac{2}{3}$; thorax with anepisternum setulose; scutellum with 4 setae and variable number of setulae between them; abdomen with tip as illustrated in Fig. 245. . . . . *Phlebothrix* Borgmeier

– Wing with at most single setula on vein R_1; without other above combination of characters 110

110. Wing vein R_{4+5}, apart from 1–3 (usually 1) setulae at base, with additional row of usually finer setulae along upper surface (e.g., Fig. 114) 111
– Wing vein R_{4+5} with 0–3 setulae at base only 118
111. Mid tibia with pair of setae (1 dorsal and 1 near-dorsal) in basal ½ (as in Fig. 142) 112
– Mid tibia without isolated setae in basal ⅔ 116
112. Wing vein R_{2+3} present (e.g., Fig. 99) 113
– Wing vein R_{2+3} absent (e.g., Fig. 81) 114
113. Thorax with anepisternum setulose. . . . . *Borophaga* Enderlein [in part]
– Thorax with anepisternum bare. 118
114. Hind tibia with 1 or 2 dorsal or near-dorsal longitudinal rows of palisade setae (e.g., Figs 168, 169). . . 115
– Hind tibia without longitudinal palisade setae, but may be row of spaced, differentiated setulae (e.g., Fig. 152) 119
115. Posterior ocelli clearly closer to anterior ocellus than to eye; ocellar region not clearly bounded in front by sinuous furrow . . . . . *Borophaga* Enderlein [in part]
– Posterior ocelli clearly closer to eye than to anterior ocellus; ocellar region usually clearly bounded in front by sinuous furrow and frons with several setae (Fig. 21) . . . . . *Stichillus* Enderlein
116. Head with frons with 1 pair of setae only (supra-antennal setae); wing and anepisternum not as described below; abdominal tergites 3–6 largely represented by setae . . . . . *Euryphora* Schmitz
– Head with frons with at least 14 setae; wing with maximum breadth less than length of costal vein (C); thorax with anepisternum setulose; abdominal tergites 5 and 6 fused, so only 5 tergites on segments 1–6 . . . . . *Plethysmochaeta* Schmitz
117. Costal wing vein (C) clearly < ½ length of wing; head with frons with 8 setae between supra-antennal setae and ocelli; body not obviously flattened dorsoventrally, so anterior thoracic spiracles positioned at margins . . . . . *Brachyselia* Schmitz
– Costal wing vein (C) clearly > ½ wing length; head with frons with at most single pair of setae below anterior ocellus; body somewhat flattened dorsoventrally, so anterior thoracic spiracles positioned dorsally 118
118. Compound eye with greatest diameter (height) < 1.5 × length of antennal postpedicel and (viewed from above) eye extending < ½ length of frons . . . . . *Euryplatea* Schmitz
– Compound eye with greatest diameter (height) at least 2 × length of antennal postpedicel and (viewed from above) eye extending full length of frons . . . . . *Microplatyphora* Schmitz
119. Mid tibia with pair of setae (1 dorsal and 1 near-dorsal) in basal ½ (e.g., Fig. 142) 120
– Mid tibia without pair of setae in basal ½, but occasionally a single setae present. 128
120. Hind tibia with at least 1 dorsal or near-dorsal, longitudinal row of palisade setae (e.g., Figs 168, 171, 172). 121
– Hind tibia without longitudinal palisade setae, but may be row of spaced, differentiated setulae (e.g., Fig. 170) 125
121. Wing vein R_{2+3} present (e.g., Fig. 72) 122
– Wing vein R_{2+3} absent (as in Fig. 73). 124
122. Thorax with anepisternum with setulae; wing with axillary ridge with 1 seta; hind tibia with 1 longitudinal row of palisade setae (Fig. 169); abdominal tergite 7 typically well-developed laterally, but middle ⅓ or more absent (Fig. 224); distiproboscis elongated . . . . . *Dohrniphora* Dahl
– Thorax with anepisternum bare, or if with setulae in upper part, then wing with alular ridge with several setae 123
123. Without below combination of characters; hind tibia with 2 or more longitudinal rows of palisade setae (Fig. 168); wing with 2 or more alula setae (Fig. 72) . . . . . *Diplonevra* Lioy [in part]
– Head, thorax and abdomen somewhat flattened dorsoventrally, with anterior thoracic spiracles dorsal in position; compound eyes somewhat reduced; hind tibia with anteroventral row of spines before apical spur; wing not as described above . . . . . *Synaptophora* Brown
124. Hind tibia with 2 dorsal, or near-dorsal, longitudinal rows of palisade setae (as in Fig. 168); palpus 2-segmented; wing vein R_1 as illustrated in Fig. 72 . . . . . *Diplonevra* Lioy [in part]

– Hind tibia with 1 dorsal, longitudinal row of palisade setae; palpus 1-segmented; wing vein R_1 typically as illustrated in Fig. 117 . . . . . .*Hypocerides* Schmitz

125. Wing with 1 seta on alular ridge and very long, branched setulae (Fig. 120) . . . . . *Beyermyia* Disney

– Wing without seta or setulae on alular ridge, or with only short setulae 126

126. Thorax with anepisternum setulose; head with frons without median furrow . . . . .*Mannheimsia* Beyer

– Thorax with anepisternum bare; head with frons with median furrow 127

127. Hind tibia with 1 (Fig. 165) or (rarely) 2 anterodorsal setae (the second inserted near lower dorsal seta); wing with subcostal vein (*Sc*) usually clearly not reaching vein R_1 (if with 2 anterodorsal setae on hind tibia, then veins *Sc* and R_1 invariably free) . . . . . .*Conicera* Meigen

– Hind tibia with only 1 anterodorsal seta in upper $\frac{2}{3}$; wing with costal sector 1 subequal to or clearly shorter than sector 2, as tips of veins R_1 and R_{4+5} widely separated . . . . . .*Gymnoptera* Lioy

128. Hind tibia with at least 1 dorsal, or near-dorsal, longitudinal row of palisade setae (as in Figs 168, 172) 129

– Hind tibia without longitudinal rows of palisade setae, but may be row of spaced, differentiated setulae (as in Fig. 170) 151

129. Wing vein R_{2+3} absent 130

– Wing vein R_{2+3} present. 135

130. Fore tarsal segments 1–4 or 1–3 asymmetrically widened (Fig. 137) and tarsal segment 5 of all legs tapered (Figs 166, 173); thorax with anepisternum with a few setulae; antenna as illustrated in Fig. 34; abdomen with terminal segments as illustrated in Fig. 243 . . . . . .*Plastophorides* Beyer

– Fore tarsal segments not asymmetrically widened and tarsal segment 5 rarely tapered, but if so, then thorax with anepisternum bare; antenna and abdomen segments not as illustrated above 131

131. Compound eyes greatly enlarged, almost meeting below and lower ommatidia markedly larger than those above (Fig. 16); legs slender (Figs 131, 148); ovipositor sheath of elaborate form (Figs 235, 236, 249). . . . . .*Veranophora* Disney [in part]

– Without above combination of characters 132

132. Thorax with anepisternum setulose 133

– Thorax with anepisternum bare 134

133. Without below combination of characters; wing veins R_1 and R_{4+5} divergent; costal sector 1 distinctly $< 3 \times$ length of costal sector 2 (Fig. 2). . . . . *Megaselia* Rondani [in part]

– Wing as illustrated in Fig. 82; head with frons with setulae (Fig. 11); upper supra-antennal setae reduced in size, displaced to position above antial setae (Fig. 11); antenna as illustrated in Fig. 29; palpus as illustrated in Fig. 53; abdomen with terminal segments modified, forming needle-like ovipositor and sheath (Fig. 242); fore tarsal segment 5 longer than segment 5 on all legs. . . . *Miclepta* Disney [in part]

134. Abdominal tergite 6 with embayment of front margin embracing roughly pear-shaped, non-setulose sclerite (Fig. 234); internally, Dufour's crop mechanism very short and wide, usually darkly sclerotised, with pair of long tubules extending from middle into lumen of crop (Fig. 22) . . . . . *Woodiphora* Schmitz [in part]

– Abdominal tergite 6 and Dufour's crop mechanism (when present) not modified as described above 135

135. Costal wing vein (*C*) $< \frac{2}{5}$ wing length (e.g., Fig. 82) 136

– Costal wing vein (*C*) $> \frac{2}{5}$ wing length (e.g., Fig. 99) (NB: doubtful cases key both ways). 138

136. Antennal postpedicel usually distinctly $< 2 \times$ as long as broad, but if nearly $2 \times$ as long, then arista inserted apically (e.g., Fig. 29); hind tibia with differentiated row of posterodorsal setulae 137

– Antennal postpedicel $> 2 \times$ as long as broad, with dorsal arista clearly inserted before tip (e.g., Fig. 28); hind tibia not as described above. 139

137. Abdomen with terminal segments unmodified; hind femur with setulae differentiated . . . . . *Megaselia* Rondani [in part]

– Abdomen with terminal segments developed as somewhat dorsoventrally flattened ovipositor sheath (Fig. 242); hind femur with setulae below basal $\frac{1}{2}$ not obviously differentiated from those of anterior face . . . . . *Miclepta* Disney [in part]

138. Thorax with anepisternum bare; mid and hind tibiae with 1 or more irregular rows of palisade setae on anterior face (as Fig. 172); abdominal tergite 6 as illustrated in Fig. 234, without obviously developed ovipositor behind; internally, Dufour's crop mechanism very short and heavily sclerotised, with pair of long tubules extending from middle into lumen of crop (Fig. 22) . . . . . *Woodiphora* Schmitz [in part]

– Thorax with anepisternum setulose, sometimes also setose; mid and hind tibiae without palisade setae on anterior face; abdominal tergite 6 and Dufour's crop mechanism not as described above 145

139. Hind tibia with differentiated row of anterodorsal setulae, as well as posterodorsal row (the 2 rows separated by dorsal palisade setae). 140

– Hind tibia at most with posterodorsal row of differentiated setulae only 141

140. Either palpus or supra-antennal setae, or both, clearly longer than upper occipital setae; abdominal tergite 3 without papillae . . . . . *Megaselia* Rondani [in part]

– Palpal setae and supra-antennal setae only *ca* as strong as upper occipital setae; abdominal tergite 3 frequently with pair of oval to round papillae near anterior margin (Fig. 233) . . . . . *Phalacrotophora* Enderlein [in part]

141. Fore tibia with near-dorsal longitudinal row of palisade setae (as on mid and hind tibiae); antennal postpedicel pear-shaped, with apical arista and conus (apical bulb) of second segment seemingly inserted laterally (not basally) on postpedicel (Fig. 28); abdominal sternite 6 present, with differentiated setae at posterior margin (Fig. 226); ovipositor sheath elongated, embracing sharply pointed retractile ovipositor (Fig. 227) . . . . . *Epactoselia* Disney

– Without above combination of characters 142

142. Fore and mid legs with terminal tarsomeres at least, longer than tarsomeres 4 and usually tapered (e.g., Fig. 136) 143

– All legs with terminal tarsomeres shorter than tarsomeres 4 or longer on fore leg only. 144

143. Palpus with setae, even if short (Fig. 54); wing with costal vein (C) at most only $^{2}/_{5}$ wing length; ovipositor well-developed (Fig. 241); head with frons as illustrated in Fig. 12; antenna as illustrated in Fig. 30 . . . . . *Microselia* Schmitz

– Palpus without setae (Fig. 59); wing with costal vein (C) over $^{2}/_{5}$ wing length; ovipositor as in Figs 247, 248; head with frons not as illustrated above, without supra-antennal setae; antenna as illustrated in Fig. 39 . . . . . *Razorfemora* Disney

144. Without below combination of characters . . . . . *Megaselia* Rondani [in part]

– Hind tibia without posterodorsal row of differentiated setulae, setulae in this position no different from adjacent setulae on posterior face; abdominal tergite 6 as illustrated in Fig. 234; internally, Dufour's crop mechanism very short, heavily sclerotised, with pair of long tubules extending from middle into lumen of crop (Fig. 22) . . . . . *Woodiphora* Schmitz [in part]

145. Wing margin incised at tip of vein M_2 and posterior lobe bordering incision with dense patch of minute setulae; veins M_1 to M_4 not thinly developed (as in most phorids), but as thick as vein R_1 . . . . . *Menozziola* Schmitz [in part]

– Without above combination of characters 146

146. Hind tibia with row of differentiated anterodorsal setulae as well as posterodorsal setae (the 2 rows being separated by row of palisade setae) 147

– Hind tibia without row of differentiated anterodorsal setulae; posterodorsal setae only on hind tibia 148

147. Palpus or supra-antennal setae (or both) clearly longer than upper occipital setae; abdominal tergite 3 without oval to round papillae near fore margin. . . . . *Megaselia* Rondani [in part]

– Palpal and supra-antennal setae only *ca* as strong as upper occipital setae; abdominal tergite 3 often with pair of oval to rounded papillae near fore margin (Fig. 233) . . . . . *Phalacrotophora* Enderlein [in part]

148. Thorax with anepisternum with strong seta as well as setulae; abdominal tergites 5 and 6 clearly shorter and narrower than tergite 4; segment 5 with pair of finger-like processes laterally (Fig. 240). . . . . *Menozziola* Schmitz [in part]

– Thorax with anepisternum with similar setation; abdominal tergites 5 and 6 not shorter and narrower than tergite 4; segment 5 without pair of finger-like processes (e.g., Fig. 237). 149

149. Abdominal tergites 5 and 6 as illustrated in Figs 237; ovipositor well-developed, but cerci vestigial, without setulae (Figs 237, 238); thorax with 3 notopleural setae; scutellum with 4 setae; wing vein

R_{4+5} without setula at base; subcostal vein (*Sc*) with tip confluent with vein R_1; labella densely spinose below . . . . . *Ritchiephora* Disney

– Without above combination of characters 150

150. Terminal segments of abdomen (posterior to semicircular tergite 6), dorsoventrally flattened, broadening apically, with concave posterior margin; ovipositor much narrow and normally withdrawn . . . . . *Ceratophoromyia* Beyer

– Terminal abdominal segments and ovipositor not as described above . . . . . *Megaselia* Rondani [in part]

151. Thorax with anepisternum with a few setulae; wing vein R_{2+3} absent; basiproboscis typically obviously longer than broad; labella gradually tapering to pointed tip; palpus relatively short, leaf-like . . . . . [return to couplet 102]

– Without above combination of characters 152

152. Wing vein R_{2+3} present (*e.g.*, Fig. 99) 153

– Wing vein R_{2+3} absent (*e.g.*, Fig. 72) 154

153. Head with frons with median furrow present, but sometimes obscure, apart from setae on vertex, with 10 or 12 setae; abdominal tergite 5 as illustrated in Fig. 234; internally, Dufour's crop mechanism very short and heavily sclerotised, with pair of long tubules extending into lumen of crop (Fig. 22) . . . . . *Woodiphora* Schmitz [in part]

– Head with frons with median furrow, but setae reduced to fine setulae; abdominal tergite 5 and Dufour's crop mechanism not as described or illustrated above 154

154. Wing with costal vein (*C*) very short; veins M_1 to M_4 very pale (Fig. 75); abdominal tergite 6 not pigmented in middle ⅓ . . . . . *Danumphora* Disney [in part]

– Without above combination of characters 155

155. Abdominal tergites 1–6 absent, apart from rudiment of tergite 5, associated with gland opening; head with frons without setae between anterior ocellus and 2 supra-antennal setae; scutum clearly wider at front than at rear; wing membrane may be shed . . . . . *Termitophorina* Borgmeier

– At least abdominal tergite 2 present; head with frons not as described above; scutum similar; wing membrane intact, but may be reduced 156

156. Wing with thin veins evident; vein M_4 bent towards basal curve of vein M_2, so space between veins constricted medially (Fig. 80); compound eye and ocelli present (typical form). . . . . *Metopina* Macquart [in part]

– Wing as illustrated in Fig. 79; compound eyes absent, or represented by 1 or 2 reduced ommatidia only; ocelli absent (blind morph) . . . . . *Metopina* Macquart [in part]

Synopsis of the fauna

***Aenictacantha* Disney** (Metopininae: Metopinini)**.** A genus of three described species, occurring in the Afrotropical and Oriental Regions. The single Afrotropical species, *A. crassitarsalis*, was described from Ghana. The genus is myrmecophilous, being associated with ants of the genus *Crematogaster*, otherwise the biology and immature stages remain unknown.

***Aenigmatistes* Shelford** (Phorinae)**.** An endemic genus of 20 described species that are widely distributed in the continental Afrotropics, including Yemen in the Southern Arabian Peninsula. *Aenigmatistes reichenspergeri* Schmitz, 1953, has been reported from a *Macrotermes* Holmgren termite mound. An identification key to species was provided by Disney (1991*d*), supplemented by Disney (2006, 2015).

***Aenigmatopoeus* Schmitz** (Metopininae: Metopinini)**.** An endemic genus of six species distributed in East, Southern and West Africa. Adults are recorded from colonies of driver ants (*Dorylus*) and in termite (*Macrotermes*) colonies. An identification key to females of the six species was provided by Disney & Kistner (1997) and the males of some species were described by Colyer (1958) and Mostovski (2004).

***Aptinandria* Schmitz** (Metopininae)**.** An endemic monotypic genus, with the single described species, *A. effeminata* Schmitz, 1921, described from a female from the mountains of Kenya (Schmitz 1921). Biology and immature stages remain unknown. The male is undescribed, but was included in an identification key provided by Beyer (1965).

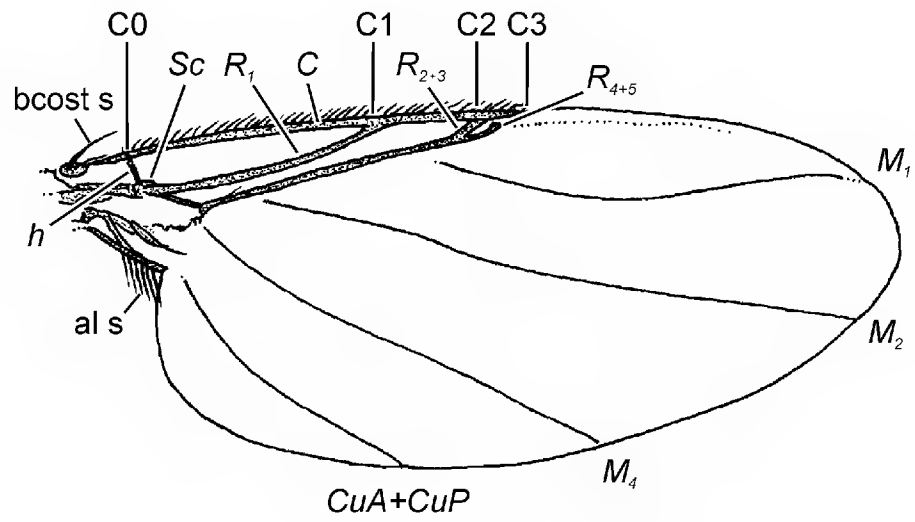
***Arabiphora* Disney** (Metopininae)**.** A monotypic genus, with the single described species, *A. tenuifemorata* Disney, 2006, recorded from Yemen in the Southern Arabian Peninsula and Palearctic Israel. Biology and immature stages remain unknown. The species is only known from the male sex and was treated by Disney (2006: 481) and Mostovski (2016).

Arrenaptenus Schmitz (Metopininae)**.** An endemic genus of two described species, *A. humilis* Borgmeier, 1959, described from Democratic Republic of Congo and *A. machadoi* Schmitz, 1958, from Angola. The males of mountain-dwelling species are flightless. Biology and immature stages remain

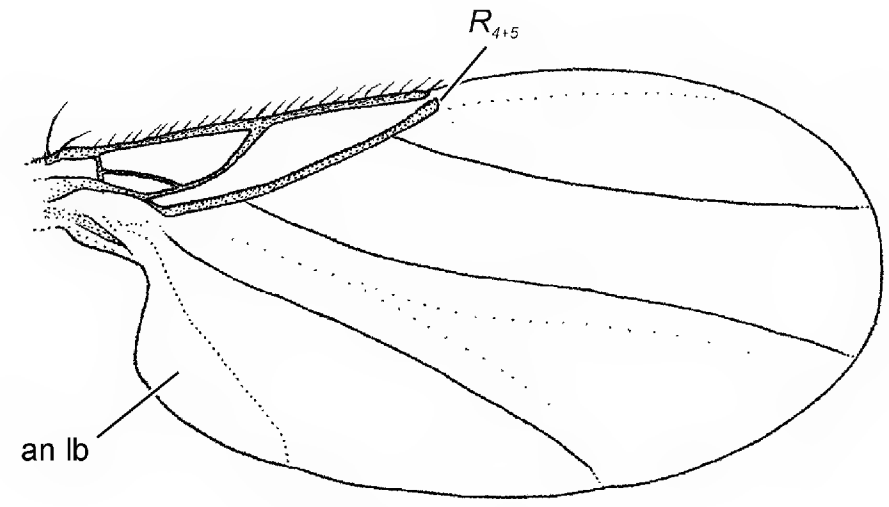
unknown. An identification key to the two species is currently unavailable.

***Beyermyia* Disney** (Phorinae)**.** An endemic, monotypic genus, with the single species, *B. sinulicosta*, described from Democratic Republic of Congo and South Africa. Adults have been reported from carcasses of Springbok and Impala by Disney (1991e), but the biology and immature stages otherwise remain unknown. The female of *B. sinulicosta* was dealt with by Beyer (1965) and the male by Disney (1991e), who added a further description of the female.

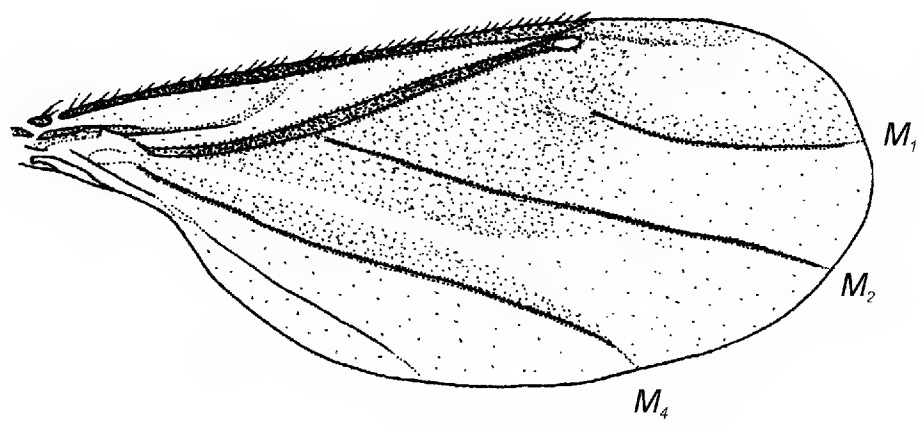
***Borophaga* Enderlein** (Phorinae: Hypocerini)**.** A genus of *ca* 30 described species, occurring in all zoogeographical regions,



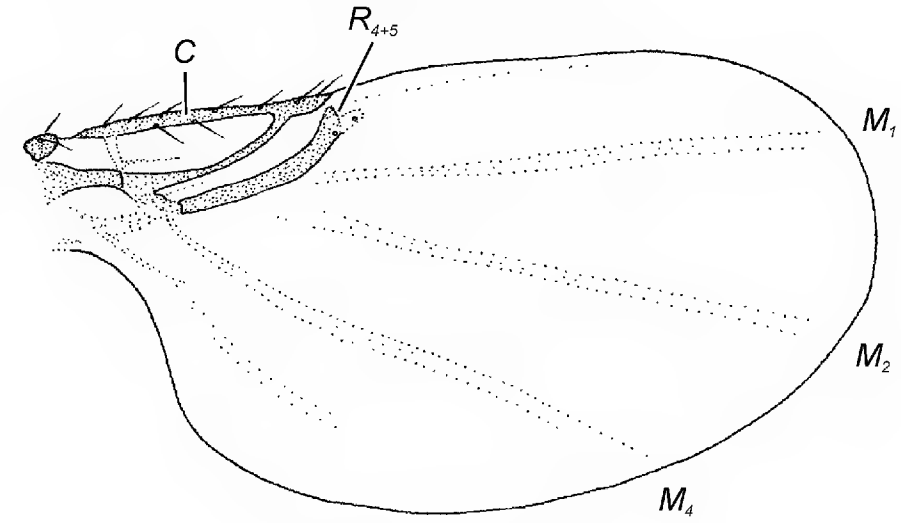
72 *Diplonevra* ♂



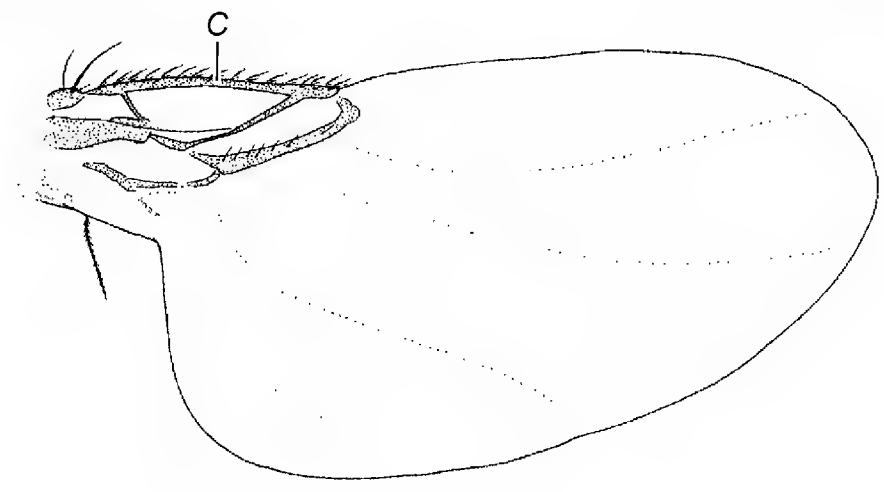
73 *Arababiphora* ♂



74 *Chonocephalus* ♂



75 *Danumphora* ♂



76 *Euryphora* ♂

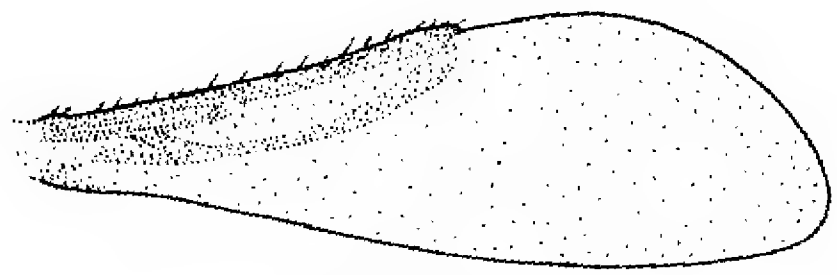
Figs 59.72–76. Wings of Phoridae (dorsal views): (72) *Diplonevra* sp. ♂; (73) *Arabiphora tenuifemorata* Disney ♂; (74) *Chonocephalus heymonsi* Strobbe ♂; (75) *Danumphora hageri* Disney ♂; (76) *Euryphora arabiensis* Disney ♂. Fig. 72 (Disney 1983*b*, fig. 57), Figs 73–76 (Disney 2006, figs 10, 20, 30, 44).

Abbreviations: al s – alula setae; an lb – anal lobe; bcost s – basicostal seta; *C* – costal vein; C0–3 – costal sections 0–3; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *h* – humeral crossvein; M_1 – first branch of media; M_2 – second branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *Sc* – subcostal vein.

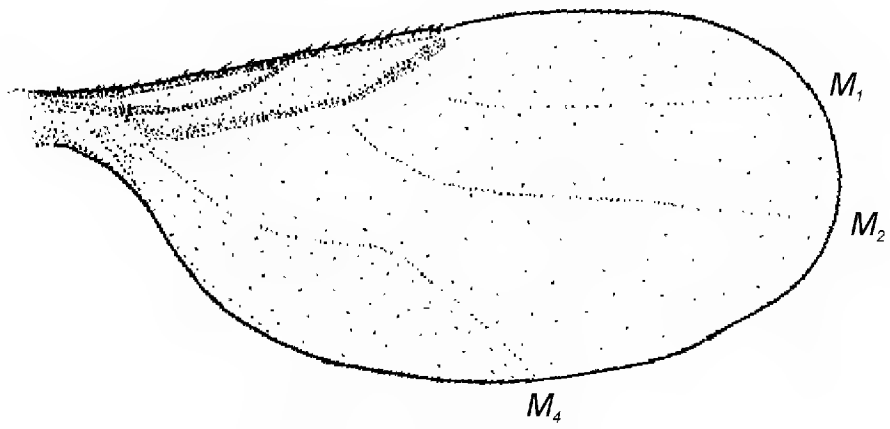
except Australasia and Antarctica. A single species, *B. rufibasis* Beyer, 1959, occurs in the Afrotropical Region, recorded from South Africa and Tanzania, which was re-described by Mostovski (2004). Brown (1992) proposed splitting the genus into four separate genera, *i.e.*, *Godavaria* Brown, *Latiborophaga* Brown and *Peromitra* Enderlein, in addition to *Borophaga sensu stricto*. The polarities of some postulated transformation series advanced in support of this proposal are in contention,

77 *Metopina* ♂

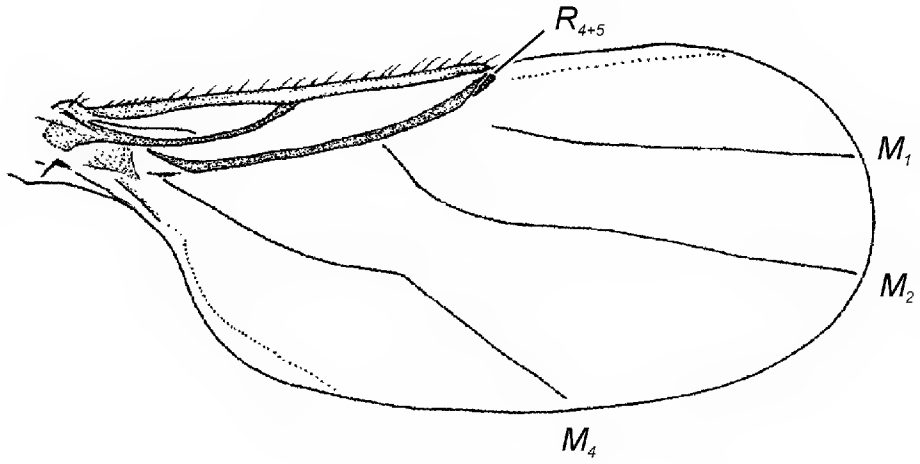
78 *Metopina* ♂



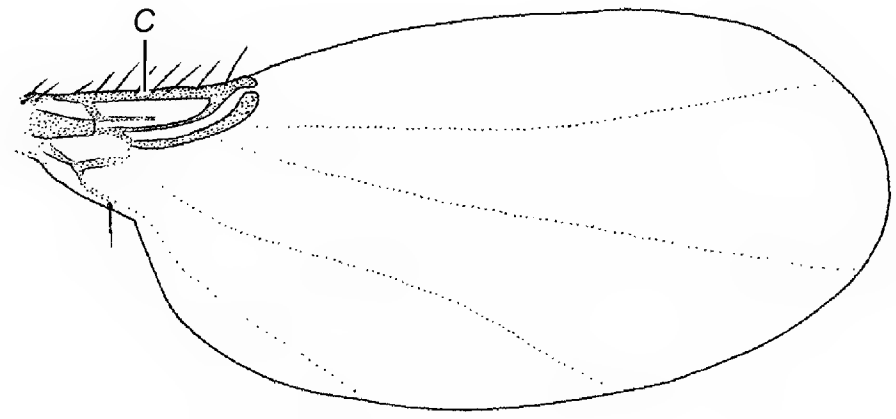
79 *Metopina* ♀



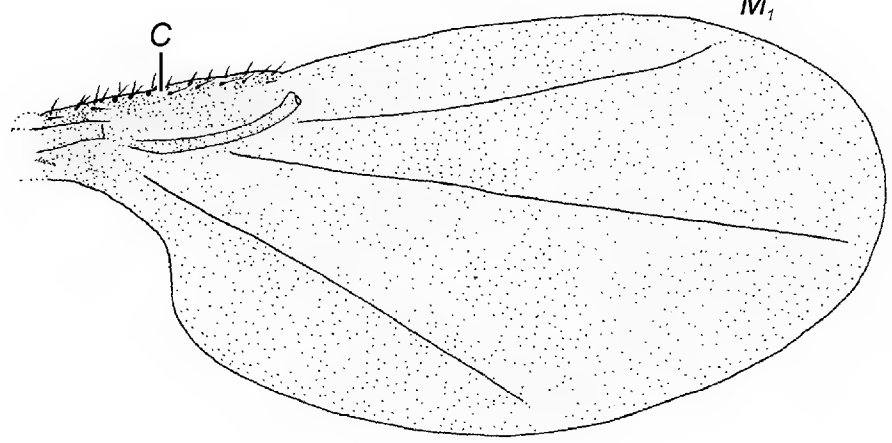
80 *Metopina* ♀



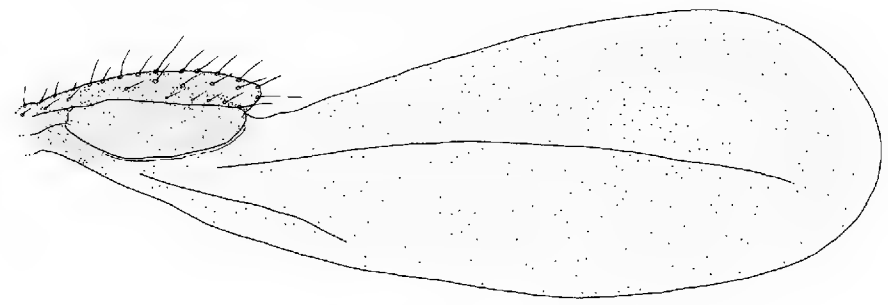
81 *Metopina* ♂



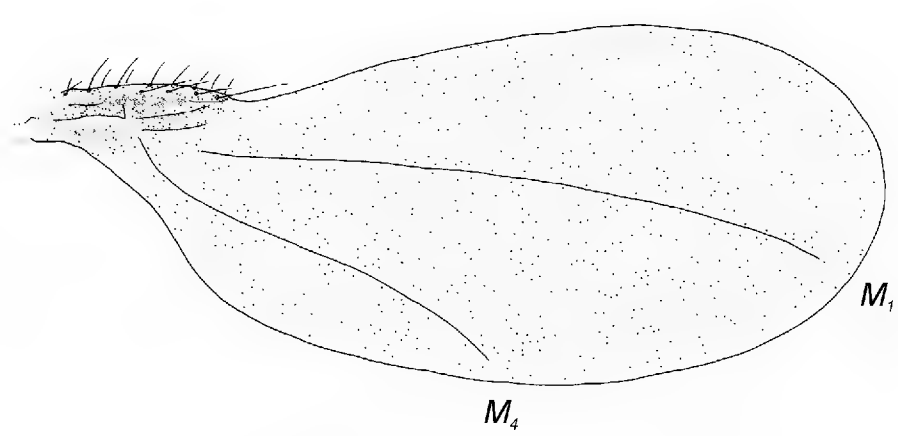
82 *Miclepta* ♀



83 *Necperissa* ♂



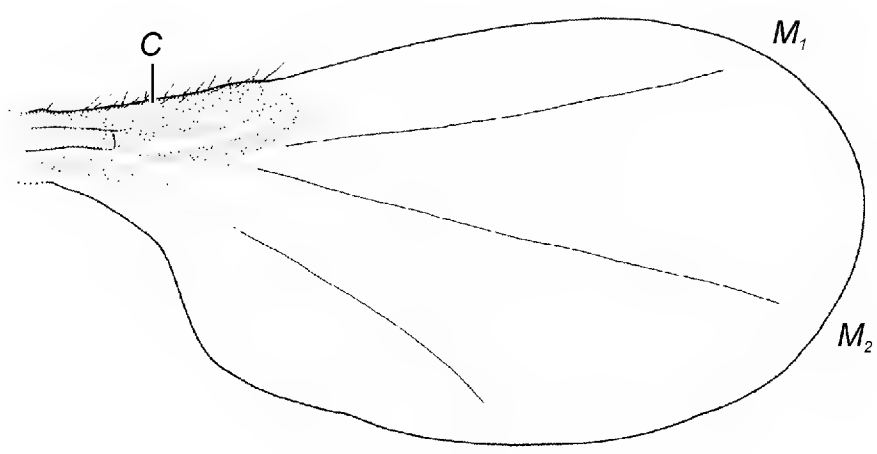
84 *Necperissa* ♀



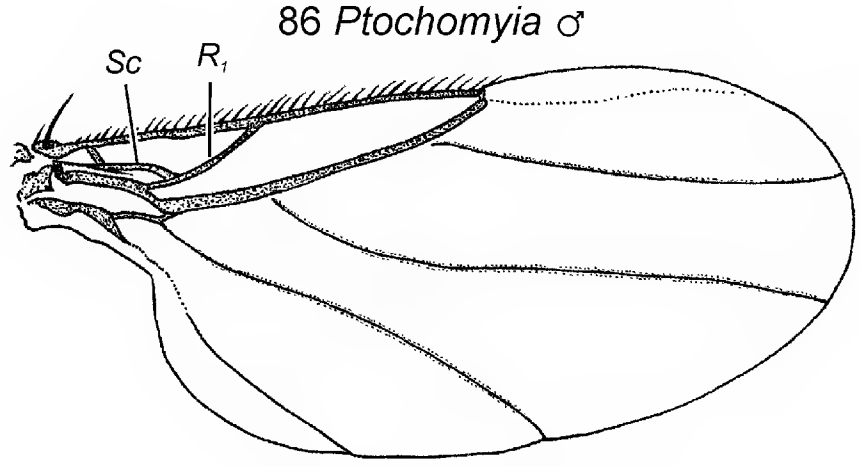
85 *Perittophora* ♀

Figs 59.77–85. Wings of Phoridae (dorsal views): (77) *Metopina ciceri* Disney ♂; (78) same ♂; (79) same (blind morph) ♀; (80) same (sighted morph) ♀; (81) *Me. heselhausi* Schmitz ♂; (82) *Miclepta arrujumensis* Disney ♀; (83) *Necperissa tinglei* Disney ♂; (84) same ♀; (85) *Perittophora couturieri* Disney ♀. Figs 77–80, 85 (Disney 1994, figs 8.59a, 8.59b, 5.2b, 5.2a, 8.69d, respectively), Figs 81, 82 (Disney 2006, figs 49, 63), Figs 83, 84 (Disney & Kistner 1995, figs 18, 19).

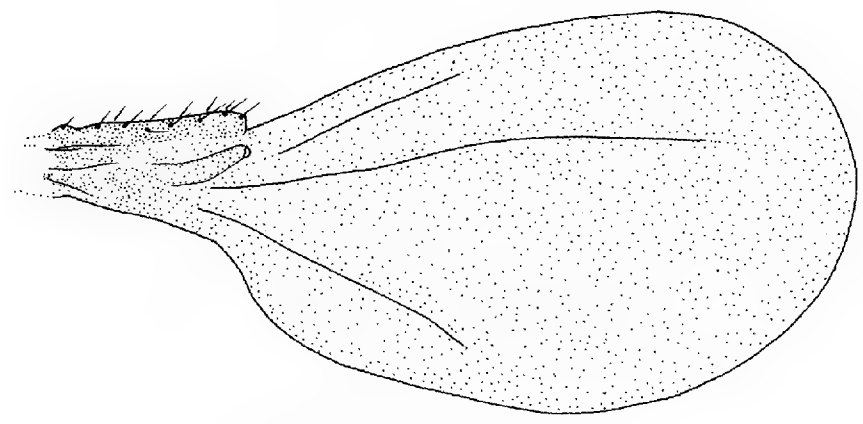
Abbreviations: *C* – costal vein; M_1 – first branch of media; M_2 – second branch of media; M_4 – fourth branch of media; R_{4+5} – third branch of radius.



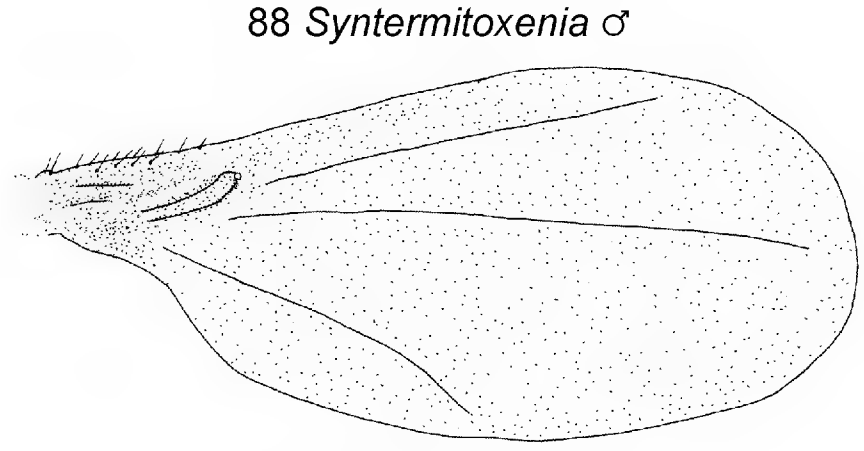
86 *Ptochomyia* ♂



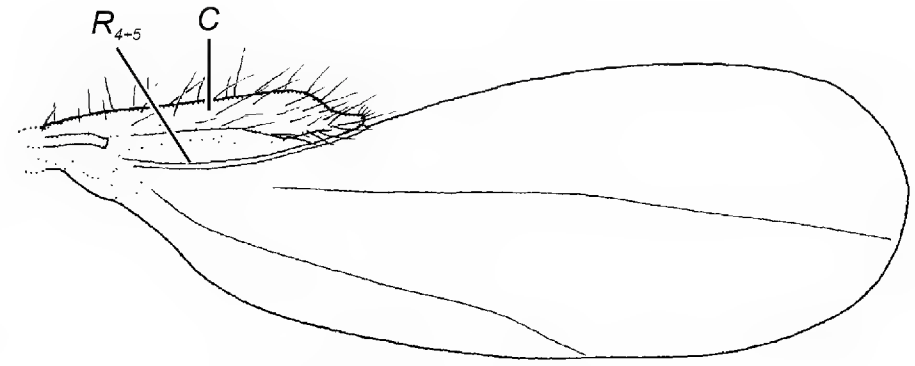
87 *Puliciphora* ♂



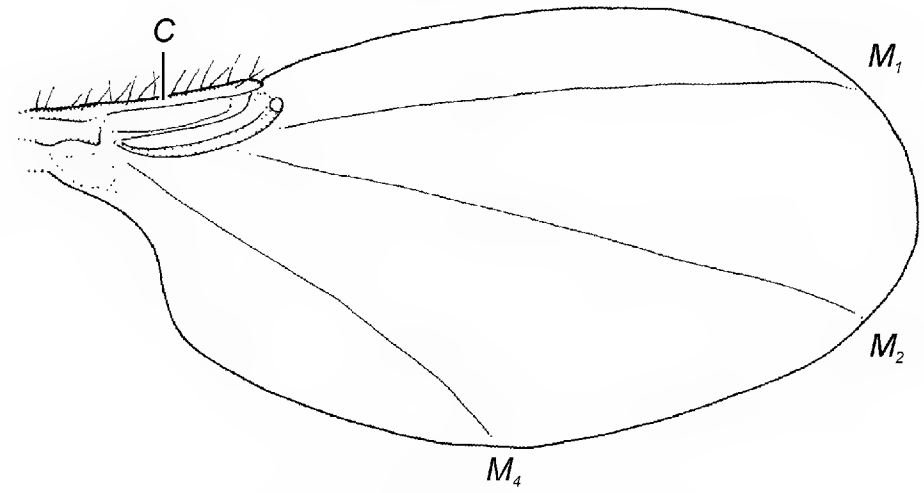
88 *Syntermitoxenia* ♂



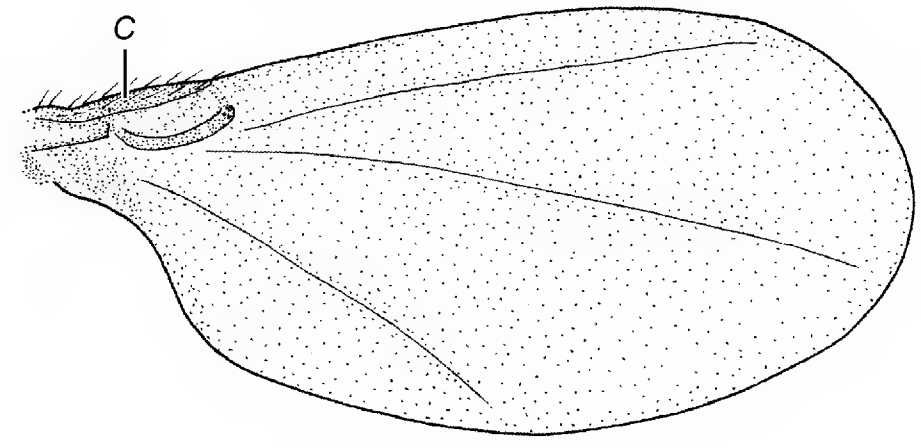
89 *Syntermitoxenia* ♂



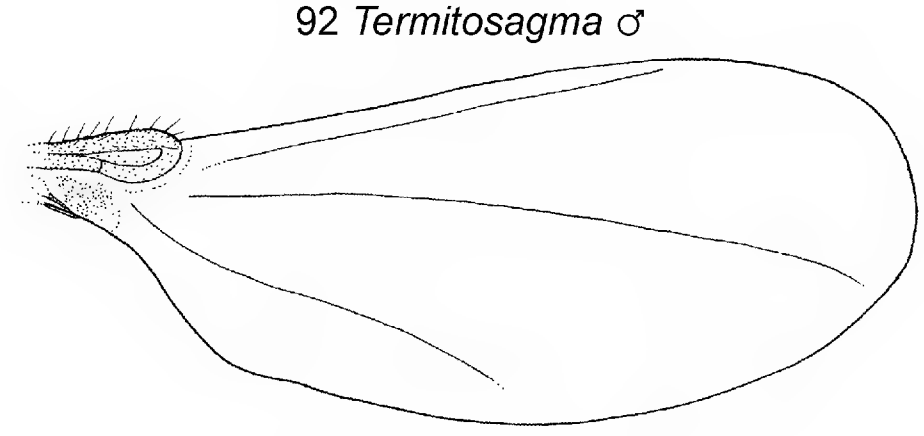
90 *Termitophilomyia* ♀



91 *Termitophilomyia* ♂



92 *Termitosagma* ♂



93 *Termitosagma* ♀

Figs 59.86–93. Wings of Phoridae (dorsal views): (86) *Ptochomyia cummingae* Disney ♂; (87) *Puliciphora borinquenensis* Wheeler ♂; (88) *Syntermitoxenia jaegerskioeldi* (Wasmann) ♂; (89) *S. lewisi* (Disney) ♂; (90) *Termitophilomyia zimbraunsi* Disney ♀; (91) same ♂; (92) *Termitosagma henningsi* Reichensperger ♂; (93) same ♀. Figs 86, 88–91 (Disney 1994, figs 8.76a, 8.82a, 8.82d, 8.85a, 8.85b), Fig. 87 (Disney 1991c, fig. 12), Fig. 92 (Disney & Darlington 2000a, fig. 9), Fig. 93 (Disney & Kistner 1995, fig. 161).

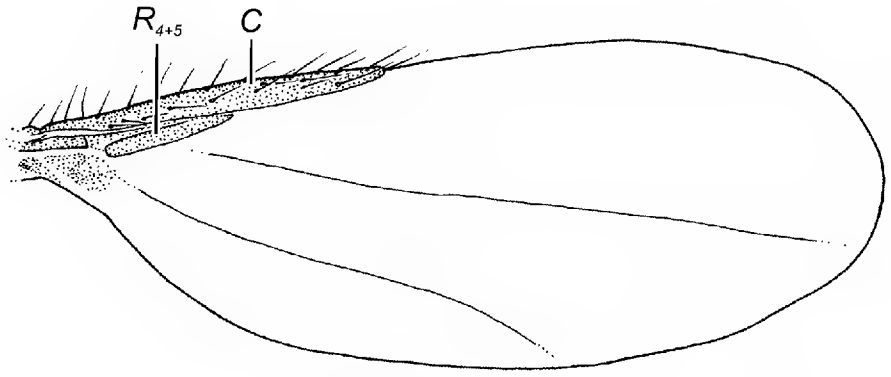
Abbreviations: *C* – costal vein; M_1 – first branch of media; M_2 – second branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; R_{4+5} – third branch of radius; *Sc* – subcostal vein.

however. For example, the presence of wing vein R_{2+3} is proposed as an autapomorphy of *Godavaria*, but this character state is undoubtedly part of the groundplan of the family, so Brown's proposal assumes the loss and subsequent re-acquisition of that vein. In view of the tentative nature of such speculations, it is considered more sensible to treat these taxa as subgenera, at least until a consensus is reached (Disney 1994: 269), although this suggestion has not been followed by some authors. Bänziger & Disney (2006) provided an identification key to these (sub)genera. Biology and immature stages remain unknown. An identification key to twenty-two of the known species (including *B. rufibasis*) was provided by Beyer (1959).

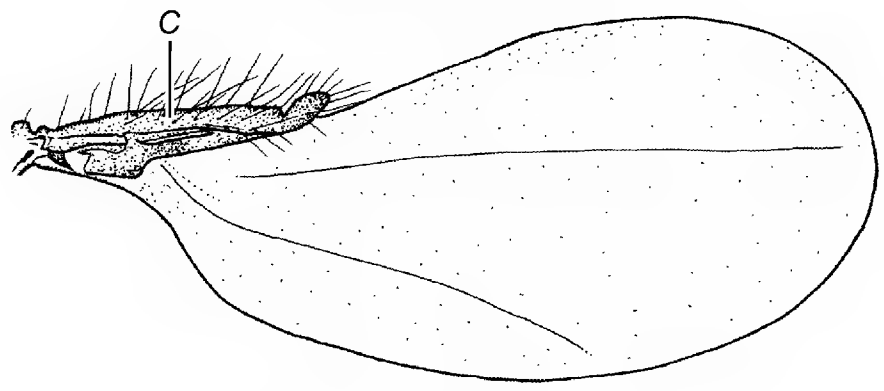
***Brachyselia* Schmitz** (Phorinae)**.** An endemic monotypic genus, with the single species, *B. natalensis* Schmitz, 1929, described from Botswana and South Africa. Previously only known from the female, the male was described by Brown (2005). Biology and immature stages remain unknown.

***Ceratophoromyia* Beyer** (Metopininae)**.** An endemic monotypic genus, with the single species, *C. pentagonalis* (Beyer, 1929), described from Angola. Biology and immature stages remain unknown.

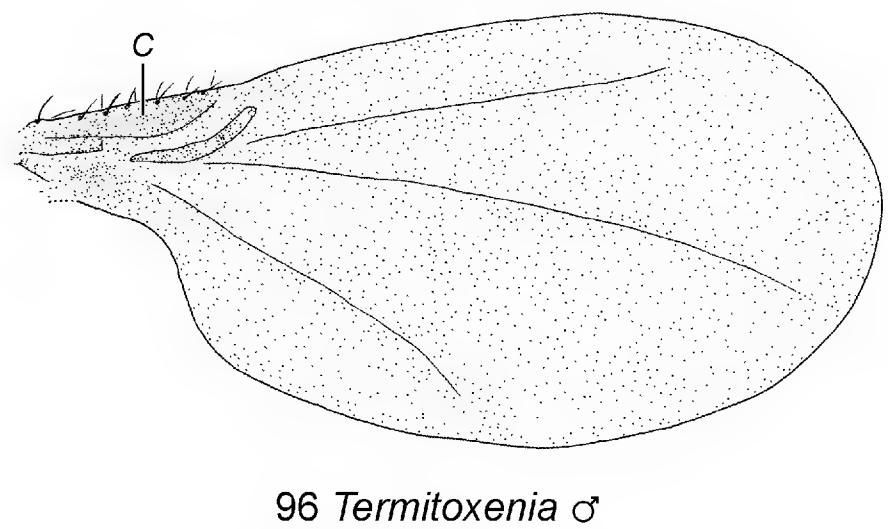
***Cheiloxenia* Delachambre** (Phorinae: Termitoxeniini)**.** An endemic monotypic genus, with the single species, *C. obesa*, described from Côte d'Ivoire. The species is currently only known from the female and was treated by Disney & Kistner (1995). Adults occur with colonies of the termite *Megaprotermes giffardii*, but the immature stages remain unknown.



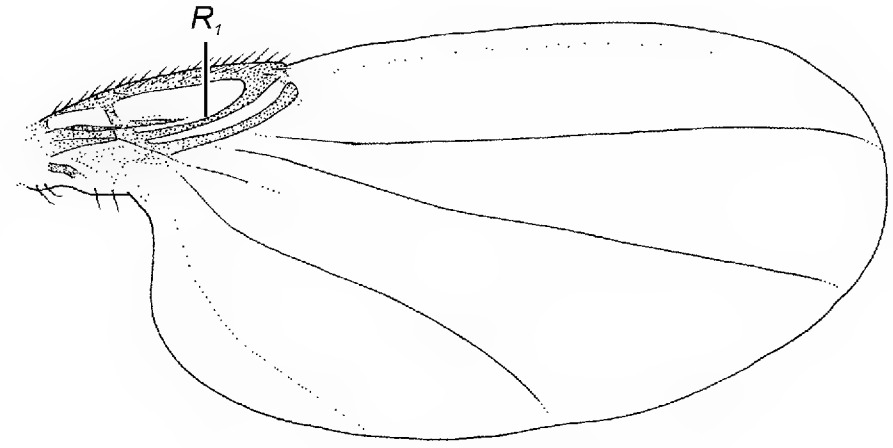
94 *Termitoscrofa* ♀



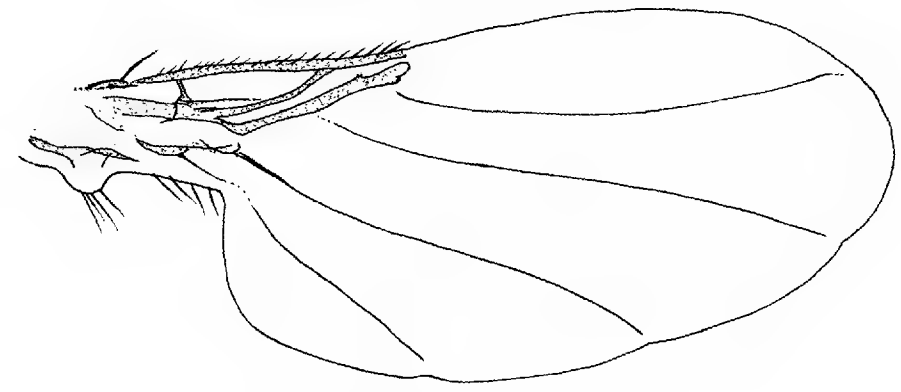
95 *Termitostroma* ♀



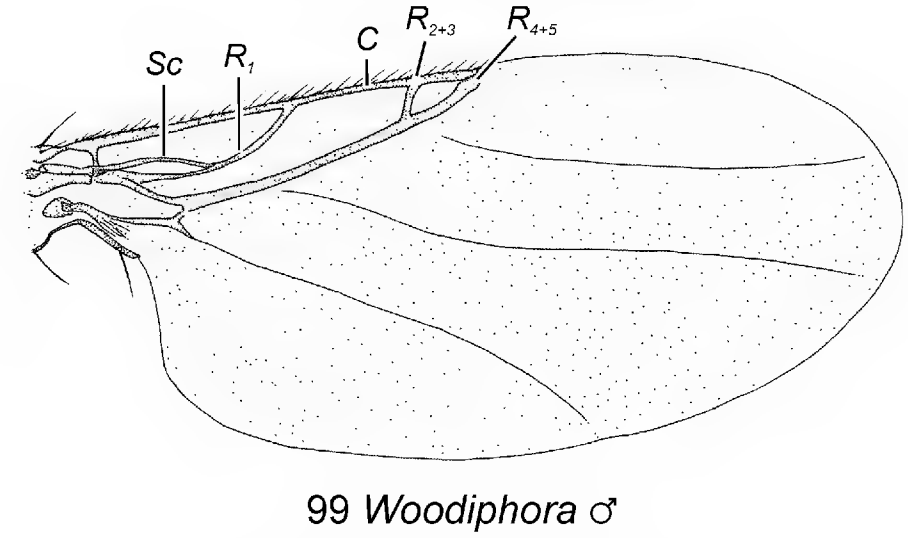
96 *Termitoxenia* ♂



97 *Thaumatoxena* ♂



98 *Veranophora* ♂



99 *Woodiphora* ♂

Figs 59.94–99. Wings of Phoridae (dorsal views): (94) *Termitoscrofa mellea* (Borgmeier) ♀; (95) *Termitostroma schmitzi* Reichensperger ♀; (96) *Termitoxenia oligoseta* (Disney) ♂; (97) *Thaumatoxena andreinii* Silvestri ♂; (98) *Veranophora medleri* (Disney) ♂; (99) *Woodiphora pallidinervis* Borgmeier ♂. Fig. 94 (Disney & Kistner 1995, fig. 124), Figs 95, 96 (Disney 1994, figs 8.86c, 8.87d), Fig. 97 (Disney & Kistner 1992, fig. 42), Fig. 98 (Disney 2006, fig. 111), Fig. 99 (Disney 1989*b*, fig. 45).

Abbreviations: *C* – costal vein; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *Sc* – subcostal vein.

***Chonocephalus* Wandolleck** (Metopininae)**.** A genus of *ca* 140 described species, occurring in all zoogeographical regions, except Antarctica, with the richest faunas in the Australasian and Oriental Regions. Several species have been transported around the world by humans and have become widely established. Fourteen species occur in the Afrotropics, distributed in East, Southern and West Africa, including Cabo Verde, Madagascar and Seychelles and United Arab Emirates and Yemen in the Southern Arabian Peninsula. The marked sexual dimorphism, along with the naming of species based on the description of a single sex, has caused much confusion. Species recognition is now based on the complex male terminalia in the first instance (Fig. 182). Identification of females requires slide mounting, in order to observe internal features of the tip of the abdomen (Fig. 219) and lone females often cannot be named. Some species exploit fungal sporophores and others have been reared from various rotting fruits and plants, otherwise the biology and immature stages remain unknown. Afrotropical species were treated by Disney (2005*a*, 2009*a*), supplemented by Disney & Aguiar (2011).

***Conicera* Meigen** (Phorinae: Hypocerini)**.** A genus of *ca* 40 described species, occurring in all zoogeographical regions, except Antarctica. Mostovski (2004) recorded the "Coffin fly", *C. tibialis* Schmitz, 1925, that breeds in corpses, especially buried human corpses, from South Africa and Beyer (1965) mentioned two undescribed species of the genus from Cameroon in the Afrotropical Region. An unnamed species is myrmecophilous, being associated with ants of the genus *Dorylus*.

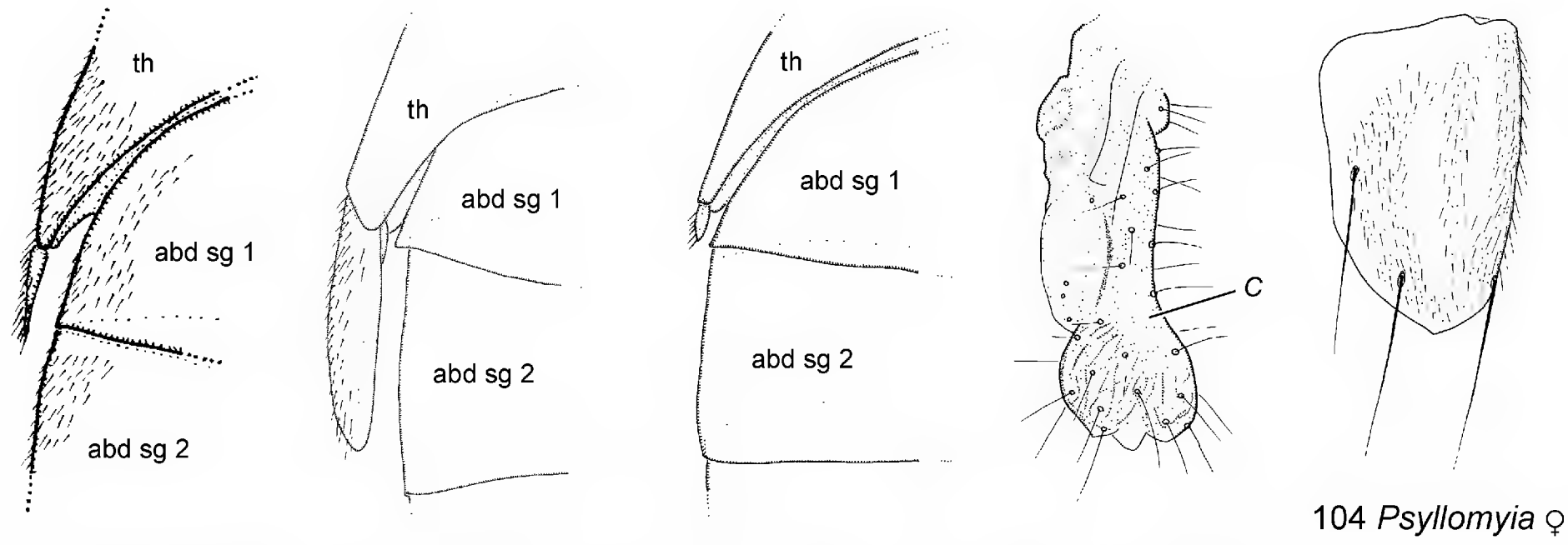
***Danumphora* Disney** (Metopininae)**.** A genus of two species occurring in the Afrotropical and Oriental Regions. One species, *D. hageri* Disney, 2006, was described from Yemen in the Southern Arabian Peninsula by Disney (2006: 487). Biology and immature stages remain unknown.

***Diplonevra* Lioy** (Phorinae: Dipolnevrini)**.** A genus of *ca* 70 species, occurring in all zoogeographical regions, except Antarctica. Twelve species occur in the Afrotropics, that are widely distributed in the continental Afrotropics. Adults of *D. brincki* are recorded from colonies of driver ants (*Dorylus*), but the immature stages remain unknown. Afrotropical species were treated by Disney & Kistner (1998), supplemented by Disney (2012*a*).

***Diplostylocera* Borgmeier** (Metopininae)**.** An endemic monotypic genus, with the single species, *D. fuscicornis* (Borgmeier, 1967), described from Democratic Republic of Congo. The species is only known from the male sex. Biology and immature stages remain unknown.

***Dohrniphora* Dahl** (Phorinae: Dipolnevrini)**.** A genus of *ca* 160 species, occurring in all zoogeographical regions, except Antarctica. Twenty species are recorded from the Afrotropics, distributed in Southern Africa and in United Arab Emirates and Yemen in the Southern Arabian Peninsula. In our current state of knowledge, most species can only be identified based on males. *Dohrniphora cornuta* breeds in decaying matter, including human corpses and adults of an unnamed species were recorded from colonies of driver ants (*Dorylus*). The immature stages of *D. cornuta* are well-documented, with the third-instar larva and puparium described by Kaneko & Furukawa (1977) and also by Kloter *et al*. (1977) and all three instars and the puparium by Feng & Liu (2012). An identification key to males of Afrotropical species was provided by Disney (2003*b*), supplemented by Disney (2006: 487) and some females were keyed by Disney & Kistner (1997).

***Dundophora* Schmitz** (Metopininae: Metopinini)**.** An endemic monotypic genus, with the single species, *D. fimbriiterga*, known from females only described from Angola (Schmitz 1955). The species is termitophagous, but immature stages remain unknown.



100 *Aenigmatistes* ♀ 101 *Aenigmatistes* ♀ 102 *Aenigmatistes* ♀ 103 *Linklloydia* ♀ 104 *Psyllomyia* ♀

Figs 59.100–104. Female wing reductions of Phoridae (dorsal views): (100) *Aenigmatistes scutellatus* (Becker); (101) *A. herero* (Enderlein); (102) *A. latifrons* Schmitz; (103) *Linklloydia ivorensis* (Delachambre); (104) *Psyllomyia braunsi* Schmitz. Fig. 100 (Disney 2006, fig. 1), Figs 101, 102, 105 (Disney 1994, figs 6.4a, 6.4b, 8.77a, respectively), Figs 103 (Disney & Kistner 1995, fig. 8), Fig. 104 (Disney & Kistner 1998, fig. 19).

Abbreviations: abd sg – abdominal segment; *C* – costal vein; th – thorax.

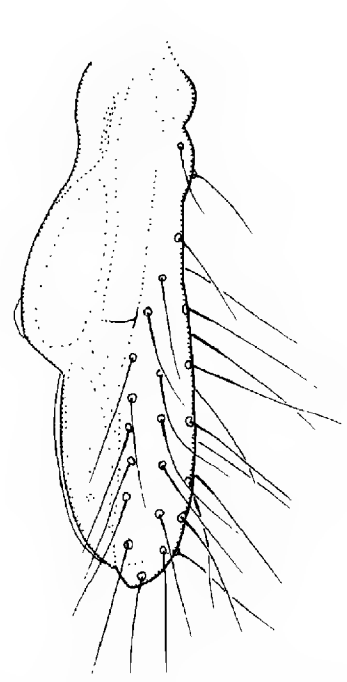
***Epactoselia* Disney** (Metopininae)**.** An endemic monotypic genus, with the single species, *E. provallaris*, known from females only, described from Tanzania. The species is myrmecophilous, associated with *Crematogaster* species, but the immature stages remain unknown. The species was treated by Disney & Kistner (1998).

***Euryphora* Schmitz** (Phorinae: Aenigmatiini)**.** An endemic genus of two species, *E. madagascarensis*, confined to Madagascar (the female described by Schmitz (1915), the male by Schmitz (1929) and *E. arabiensis* (Disney, 2006), described from Yemen in the Southern Arabian Peninsula (Disney 2006: 492). The species is myrmecophilous, associated with *Crematogaster* species, but the immature stages remain unknown. An identification key to the two species is currently unavailable.

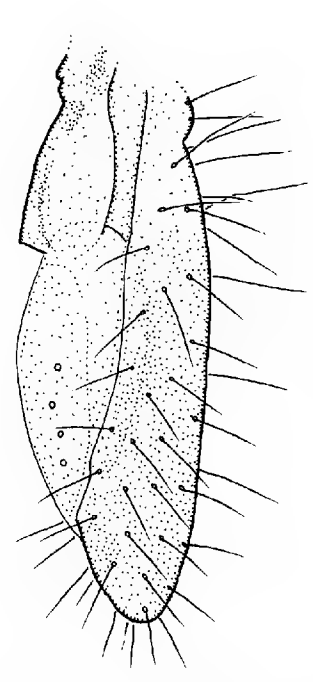
***Euryplatea* Schmitz** (Phorinae: Aenigmatiini)**.** A genus of two described species occurring in the Afrotropical and Oriental Regions (Thailand). The single Afrotropical species, *E. eidmanni*, is known only from the female, described from Bioko Island (Equatorial Guinea) (Schmitz 1941*a*). The species is myrmecophilous associated with *Crematogaster* species, but the immature stages remain unknown.

[***Godavaria* Brown.** See *Borophaga*].

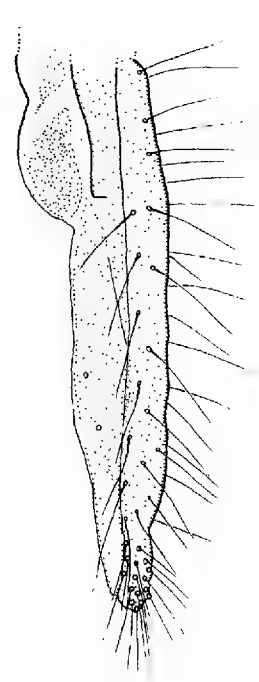
***Gymnoptera* Lioy** (Phorinae: Hypocerini)**.** A genus of three species, occurring in all zoogeographical regions, except the Nearctic Region and Antarctica. The tropical tramp species, *G. simplex*, is recorded from Nigeria and Seychelles in the Afrotropics. The larva was figured by Bohart & Gressitt (1951) and Schmitz (1953). Schmitz also referred to



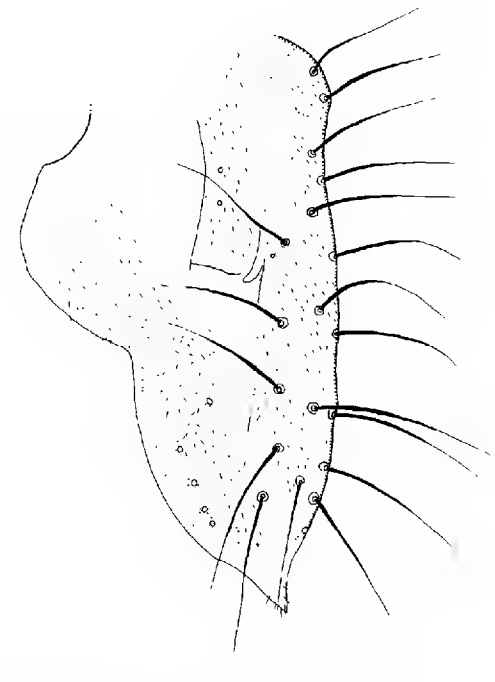
105 *Ptochomyia* ♀



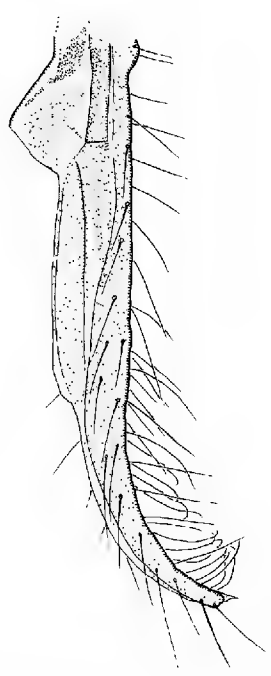
106 *Syntermitoxenia* ♀



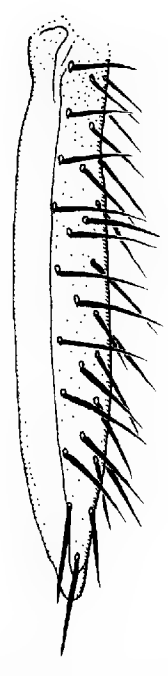
107 *Termitomyia* ♀



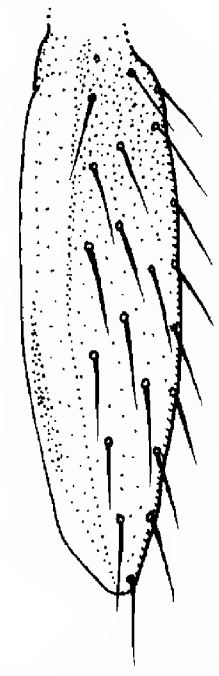
108 *Termitosagma* ♀



109 *Termitoscrofa* ♀



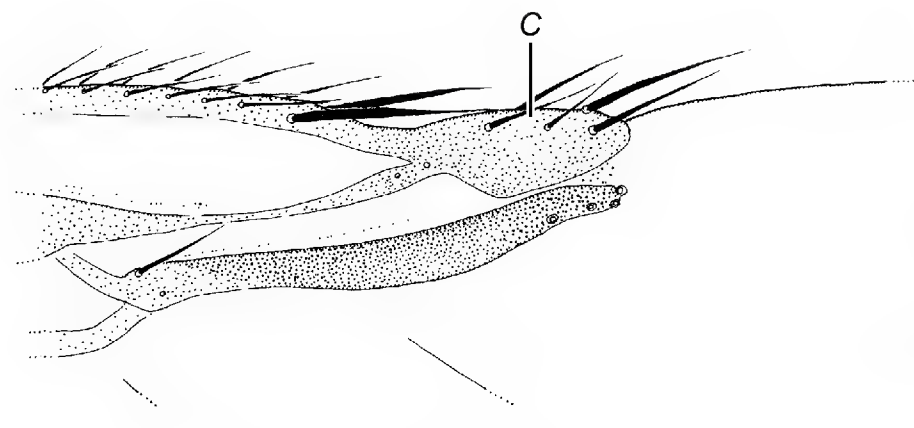
110 *Rhynchomicropteron* ♀



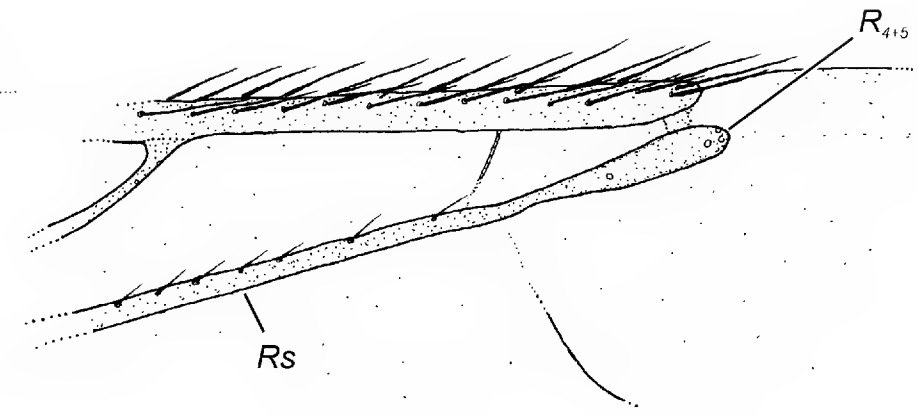
111 *Rhynchomicropteron* ♀

112 *Rhynchomicropteron* ♀

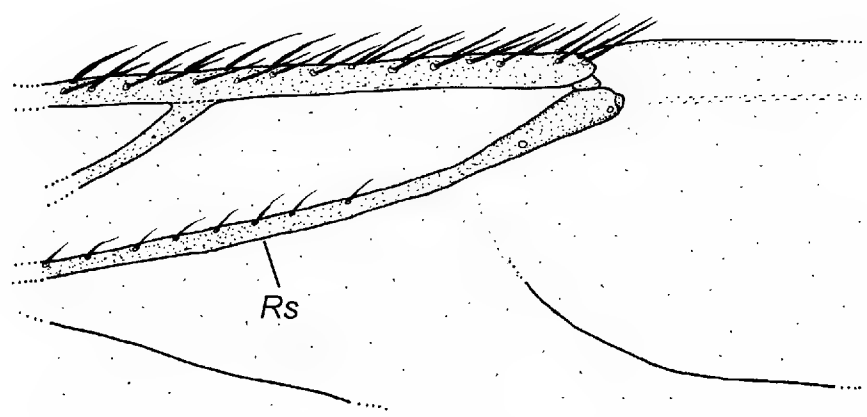
Figs 59.105–112. Female wing reductions of Phoridae (dorsal views): (105) *Ptochomyia cummingae* Disney; (106) *Syntermitoxenia extra* Disney; (107) *Termitomyia mirabilis* (Wasmann); (108) *Termitosagma henningsi* Reichensperger; (109) *Termitoscrofa pinguissima* Reichensperger; (110) *Rhynchomicropteron* sp. (non-Afrotropical); (111) same; (112) same. Figs 106, 107, 109 (Disney & Kistner 1995, figs 53, 72, 130), Figs 105, 108 (Disney 1994, figs 8.77a, 8.84e), Figs 110–112 (Disney 1999, figs 1–3).



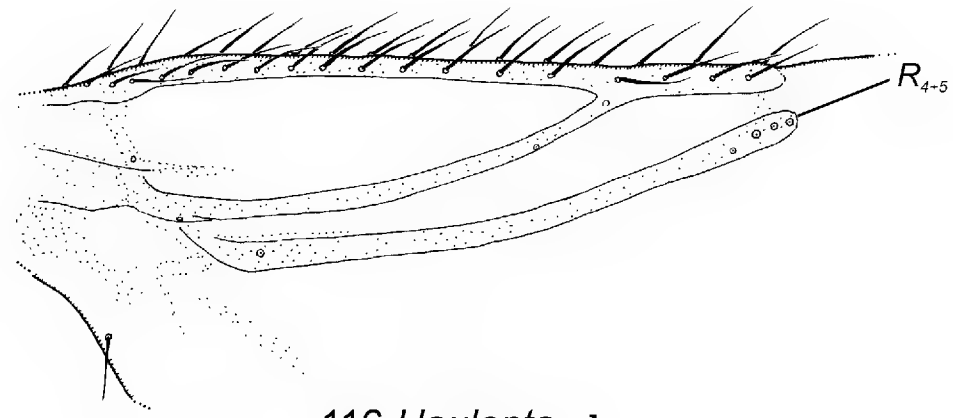
113 *Beyermyia* ♂



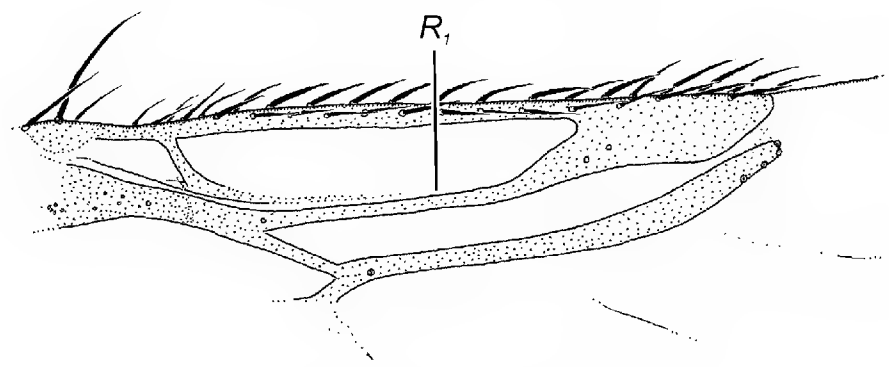
114 *Borophaga* ♂



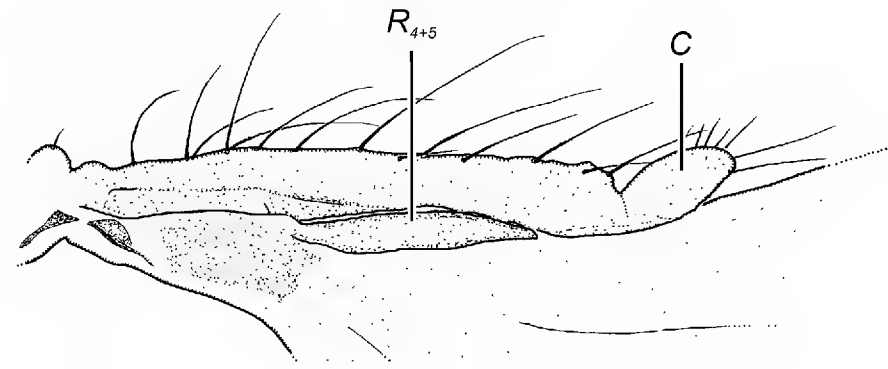
115 *Borophaga* ♂



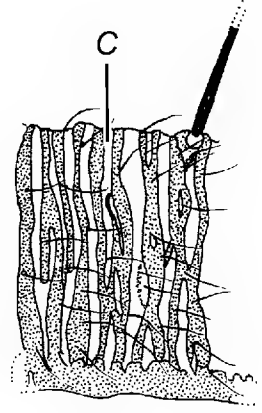
116 *Haulepta* ♂



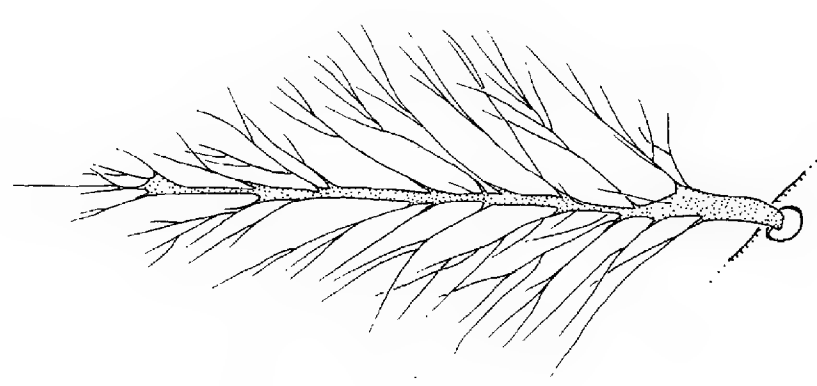
117 *Hypocerides* ♂



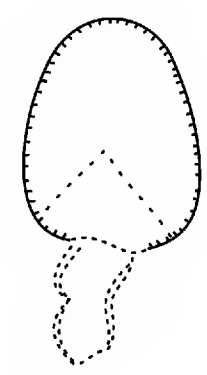
118 *Termitostroma* ♀



119 *Termitoscrofa* ♀



120 *Beyermyia* ♂



121 *Ptochomyia* ♀

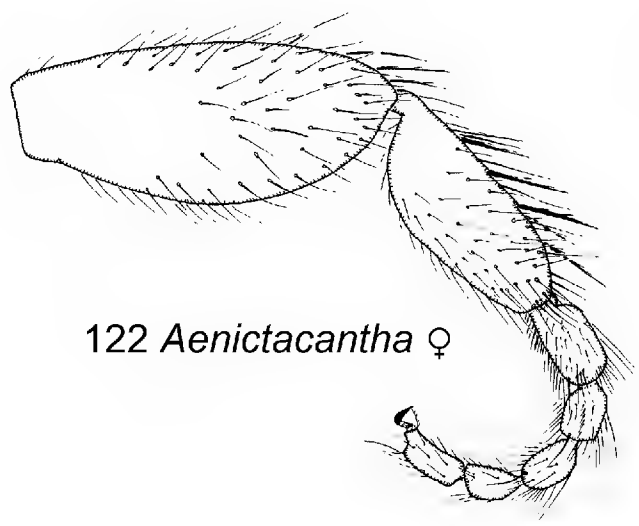
Figs 59.113–121. Wing features of Phoridae: (113) base of wing of *Beyermyia spinulicosta* (Beyer), dorsal view ♂; (114) same, *Borophaga* sp. ♂; (115) same; (116) same, *Haulepta sheasbyi* Disney; (117) same, *Hypocerides nearcticus* Borgmeier; (118) same, *Termitostroma schmitzi* Reichensperger ♀; (119) costal sector of *Termitoscrofa pinguissima* Reichensperger, dorsal view ♀; (120) male alula seta of *Be. spinulicosta*, dorsal view ♂; (121) female halter of *Ptochomyia cummingae* Disney, lateral view ♀. Figs 113, 117, 118, 120, 121 (Disney 1994, figs 8.29b, 8.49a, 8.86d, 8.29a, 8.77a, respectively), Figs 114, 115 (Disney 1983*b*, figs 21, 22), Fig. 116 (Disney & Kistner 1997, fig. 11), Fig. 119 (Disney & Kistner 1995, fig. 129).

Abbreviations: *C* – costal vein; R_1 – anterior branch of radius; R_{4+5} – third branch of radius; *Rs* – radial sector.

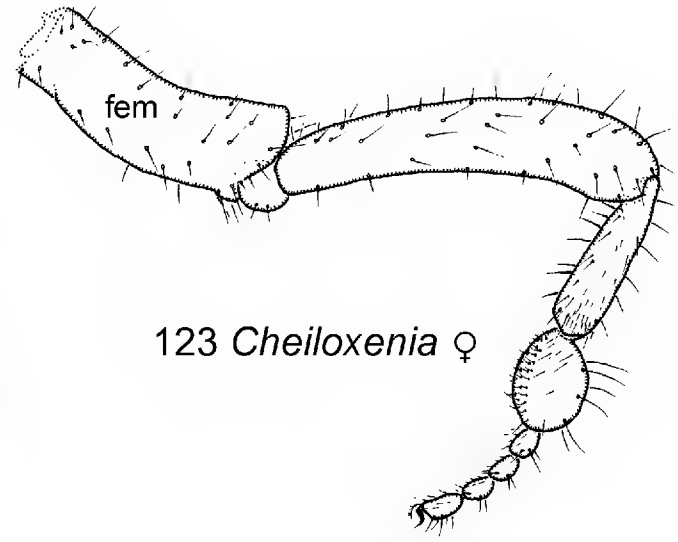
what he considered to be larval prepuparia. However, it was subsequently reported that in this species the puparium is not sclerotised, as is characteristic of Cyclorrhapha, but resembles a third-instar unsclerotised eclosion plate (Zuha & Disney 2015). Larvae have been reported feeding on dead Mollusca (Beaver 1987; Bohart 1947) and dead Coleoptera (Borgmeier 1960; Schmitz 1953) and rabbit carcasses (Zuha *et al*. 2017), adults having previously been reported on vertebrate carrion (de Meijere 1917; Disney 2003e). An identification key to the three species was provided by Disney (2003e).

***Haulepta* Disney** (Metopininae)**.** A genus of two described species occurring in the Afrotropical and Oriental Regions. The Afrotropical species, *H. sheasbyi* Disney, 1997, is only known from males and was described from South Africa. The holotype was from the nest of the termite *Odontotermes transvaalensis*. The immature stages remain unknown. The species was treated by Disney & Kistner (1997).

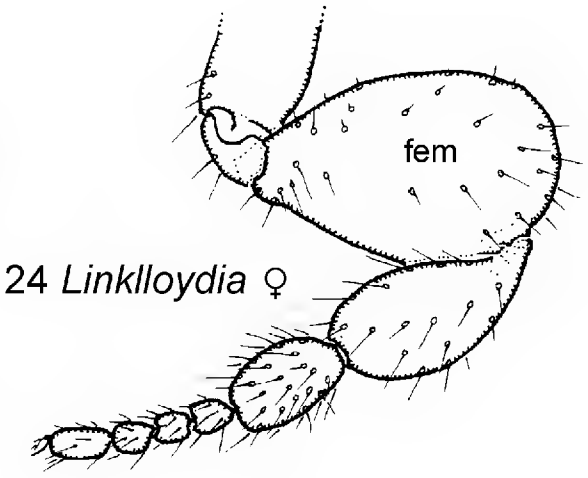
***Hexacantherophora* Schmitz** (Metopininae: Metopinini)**.** An endemic monotypic genus, with the single species, *H. cohabitans*, only known from females, described from



122 *Aenictacantha* ♀

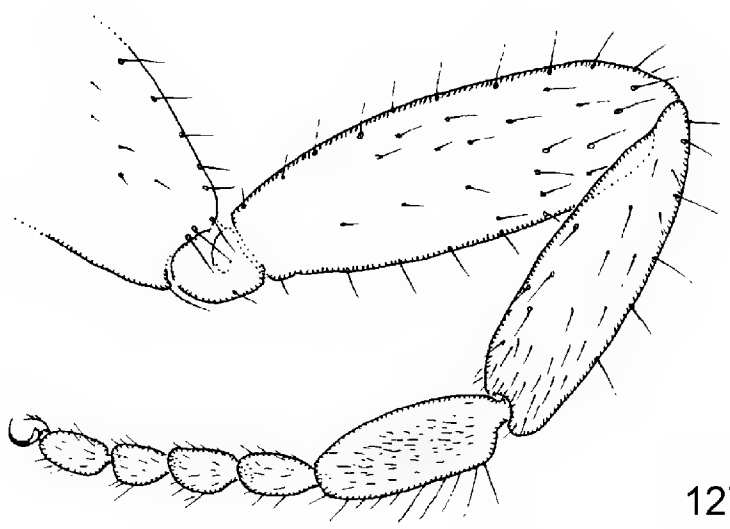


123 *Cheiloxenia* ♀

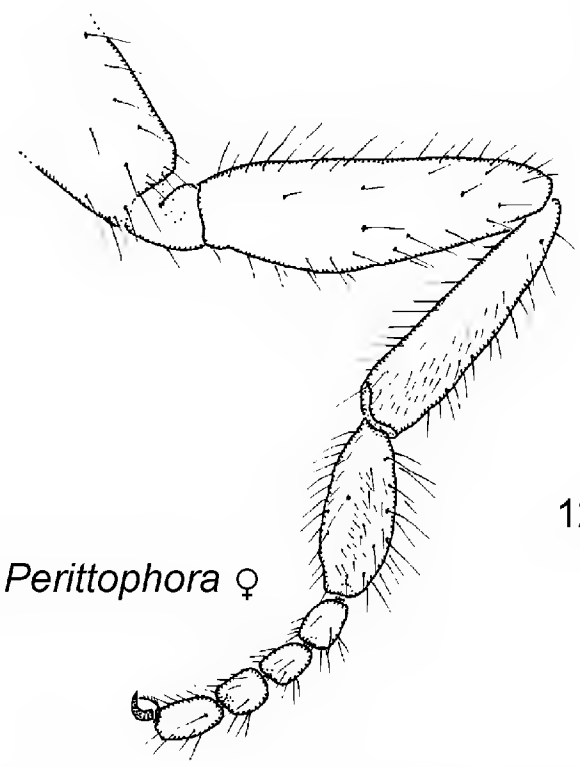


124 *Linklloydia* ♀

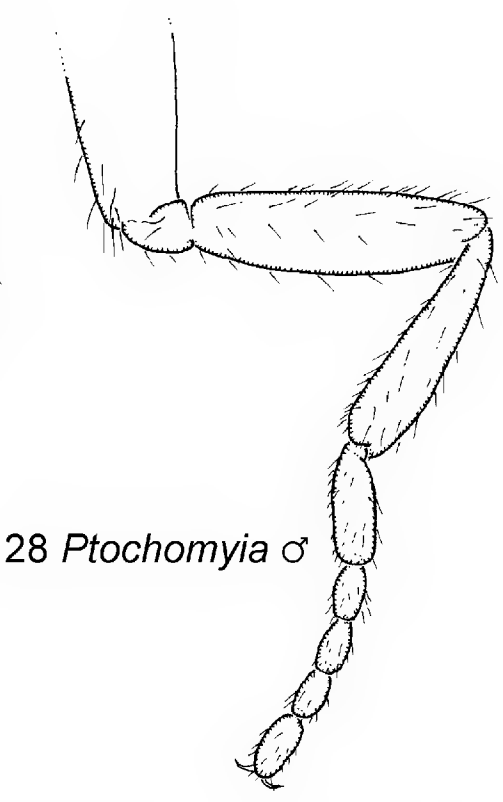
125 *Necperissa* ♂



126 *Necperissa* ♀



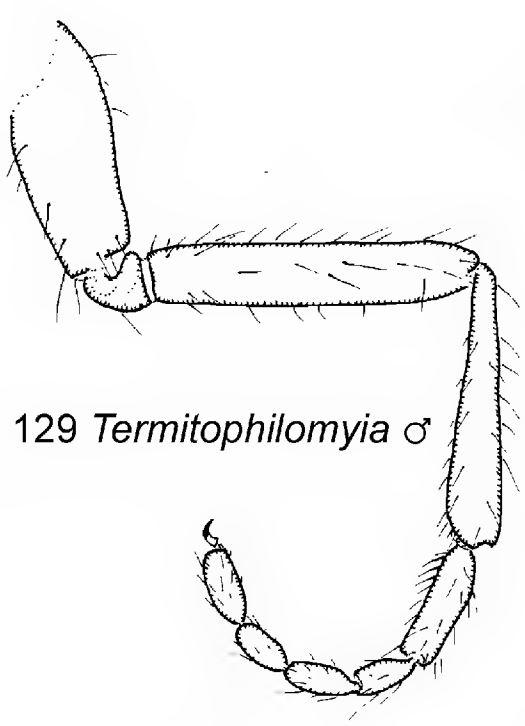
127 *Perittophora* ♀



128 *Ptochomyia* ♂

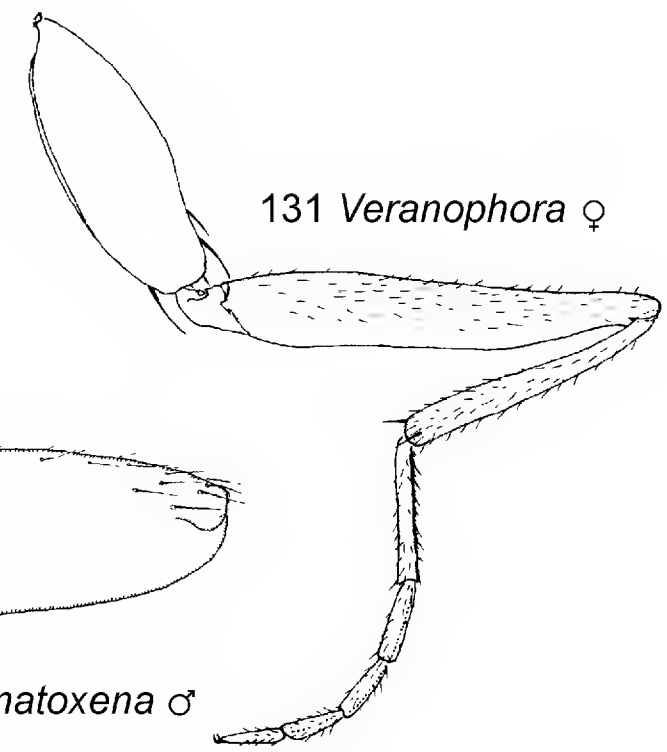
Figs 59.122–128. Fore legs of Phoridae: (122) *Aenictacantha setifera* Disney, anterior view ♀; (123) same, *Cheiloxenia obesa* Delachambre ♀; (124) *Linklloydia ivorensis* (Delachambre), posterior view ♀; (125) *Necperissa tinglei* Disney, lateral view ♂; (126) same ♀; (127) same, *Perittophora couturieri* Disney ♀; (128) same, *Ptochomyia cummingae* Disney ♂. Figs 122, 127, 128 (Disney 1994, figs 8.19b, 8.69c, 8.76c), Figs 123–126 (Disney & Kistner 1995, figs 3, 11, 17, 13, respectively).

Abbreviation: fem – femur.

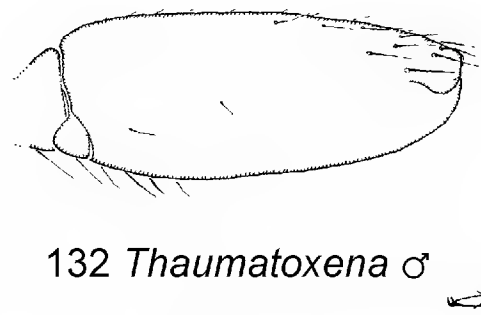


129 *Termitophilomyia* ♂

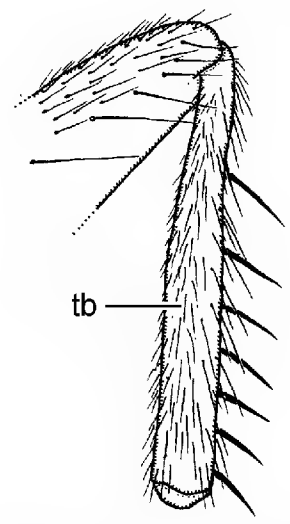
130 *Termitoxenia* ♂



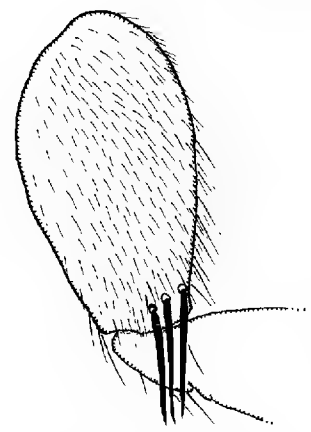
131 *Veranophora* ♀



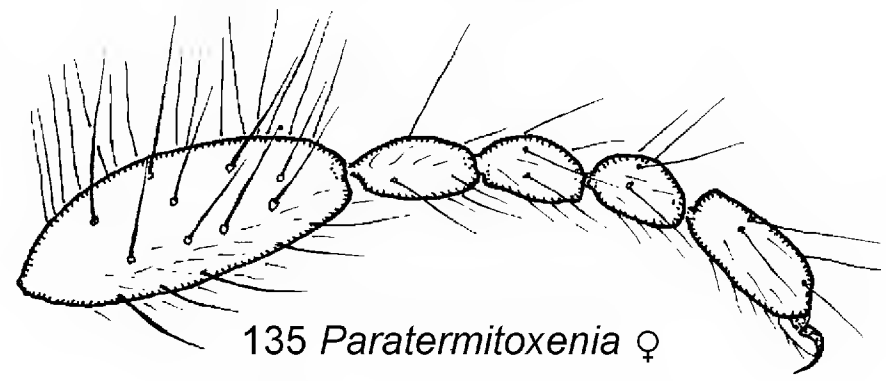
132 *Thaumatoxena* ♂



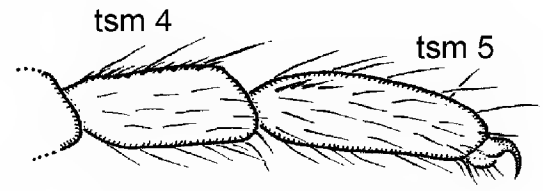
133 *Thaumatoxena* ♀



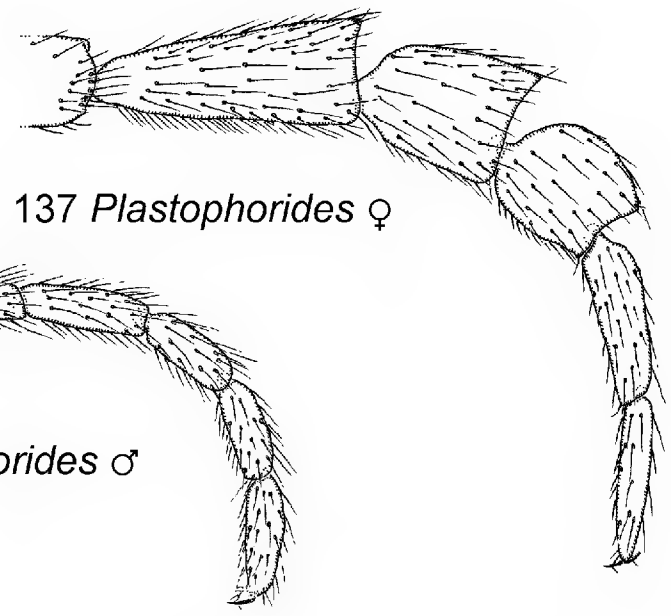
134 *Ritchiephora* ♂



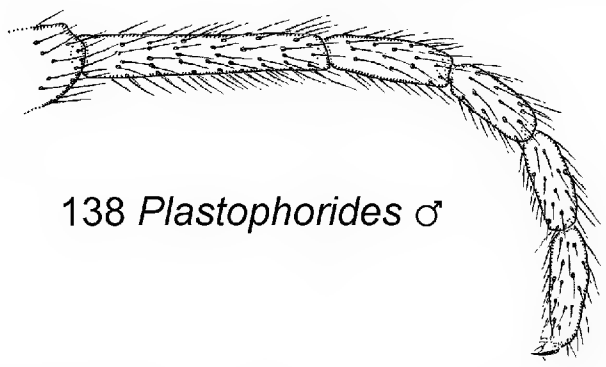
135 *Paratermitoxenia* ♀



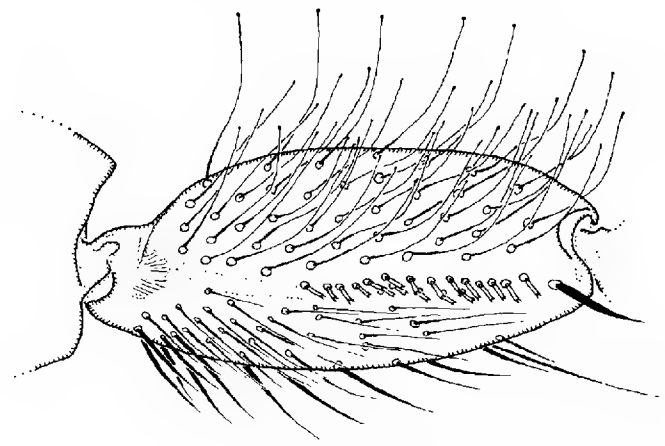
136 *Microselia* ♀



137 *Plastophorides* ♀



138 *Plastophorides* ♂



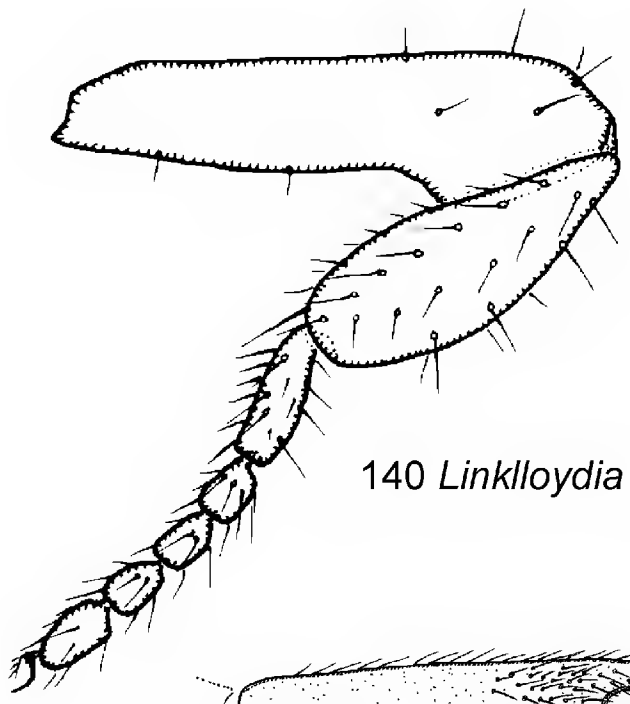
139 *Ptochomyia* ♀

Figs 59.129–139. Fore legs and leg features of Phoridae: (129) fore leg of *Termitophilomyia zimbraunsi* Disney, posterior view ♂; (130) same, *Termitoxenia oligoseta* (Disney), lateral view ♂; (131) same, *Veranophora medleri* (Disney), posterior view ♀; (132) fore femur and tibia of *Thaumatoxena andreinii* Silvestri, anterior view ♂; (133) fore femur of *Th. andreinii*, posterior view ♀; (134) fore coxa of *Ritchiephora diplopodae* Disney, lateral view ♂; (135) fore tarsus of *Paratermitoxenia coatoni* Beyer, posterior view ♀; (136) fore tarsomeres 4 and 5 of *Microselia yemenensis* Disney, lateral view ♀; (137) fore tarsus of *Plastophorides aculeipes* (Collin), lateral view ♀; (138) same ♂; (139) fore tarsomere 1 of *Ptochomyia cummingae* Disney, lateral view ♀. Figs 129, 137, 138 (Disney 1994, figs 8.85c, 8.72a, 8.72b, respectively), Fig. 130 (Disney & Kistner 1995, fig. 157), Figs 131, 136 (Disney 2006, figs 117, 71, respectively), Fig. 132 (Disney & Kistner 1992, fig. 33), Fig. 133 (Disney 2003*b*, fig. 13, as *Dohrniphora*), Fig. 134 (Disney & Ritchie 1997, fig. 2), Figs 135, 139 (Disney & Kistner 1995, figs 22, 40).

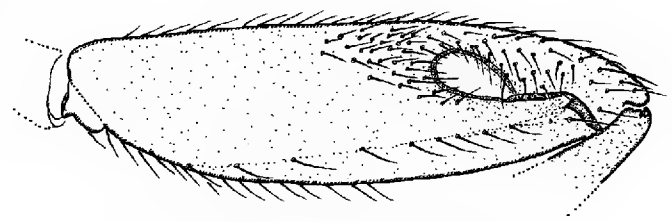
Abbreviations: tb – tibia; tsm – tarsomere.

Democratic Republic of Congo (Schmitz 1914). Adults of *H. cohabitans* are recorded from colonies of driver ants (*Dorylus*), but the immature stages remain unknown.

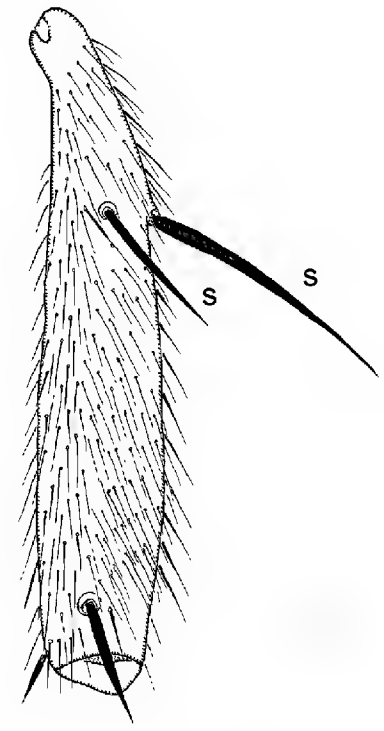
***Hypocerides* Schmitz** (Phorinae: Hypocerini)**.** A genus of seven species, occurring in the Afrotropical and Neotropical Regions and Holarctic Realm. Two species occur in the Afrotropics, the virtually cosmopolitan *H. nearcticus* Borgmeier, 1963, recorded from Kenya, Madagascar and Yemen and *H. normalis* Beyer, 1965, described from Democratic Republic of Congo. *Hypocerides nearcticus* is recorded as being a "smoke" fly, the biology and immature stages otherwise remain unknown. A preliminary identification key, that includes the two Afrotropical species, was provided by Disney (1991e).



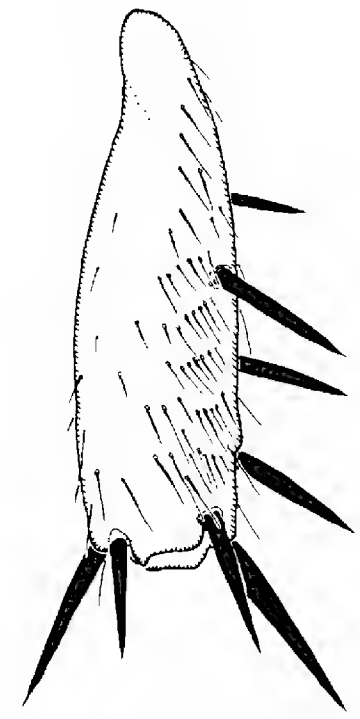
140 *Linklloydia* ♀



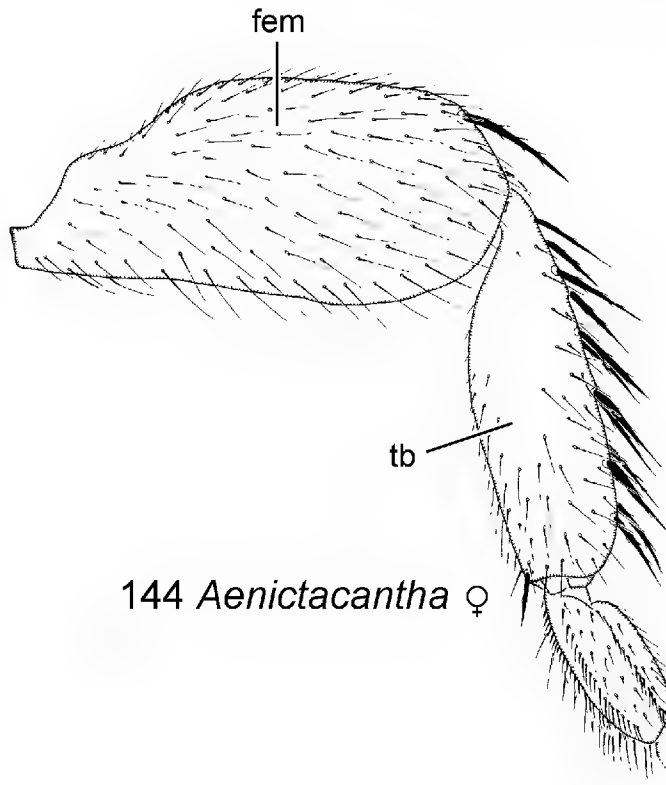
141 *Conicera* ♂



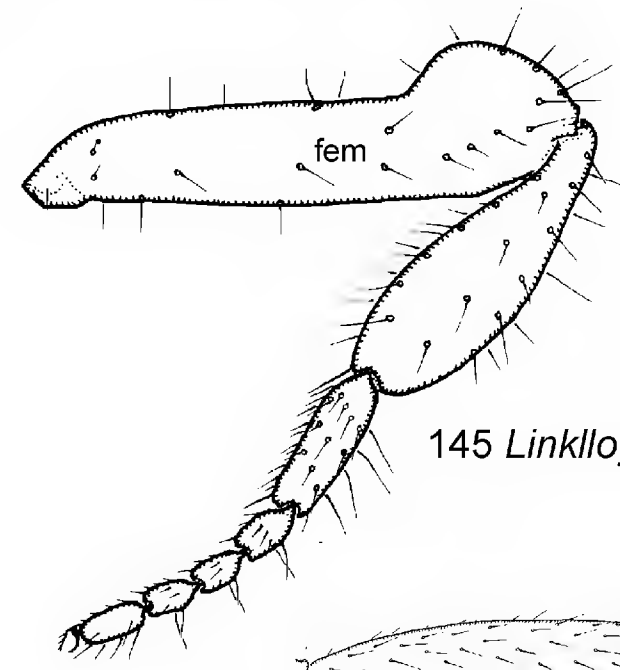
142 *Conicera* ♂



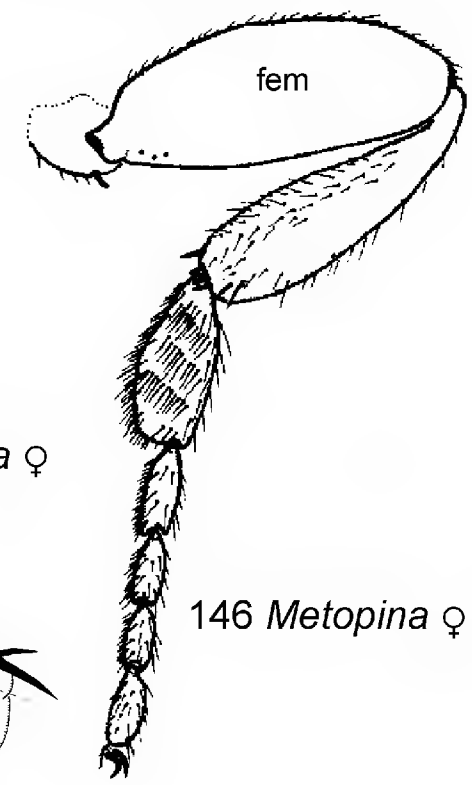
143 *Thaumatoxena* ♀



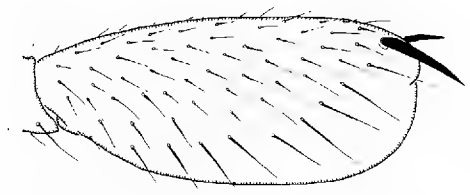
144 *Aenictacantha* ♀



145 *Linklloydia* ♀



146 *Metopina* ♀



147 *Thaumatoxena* ♀

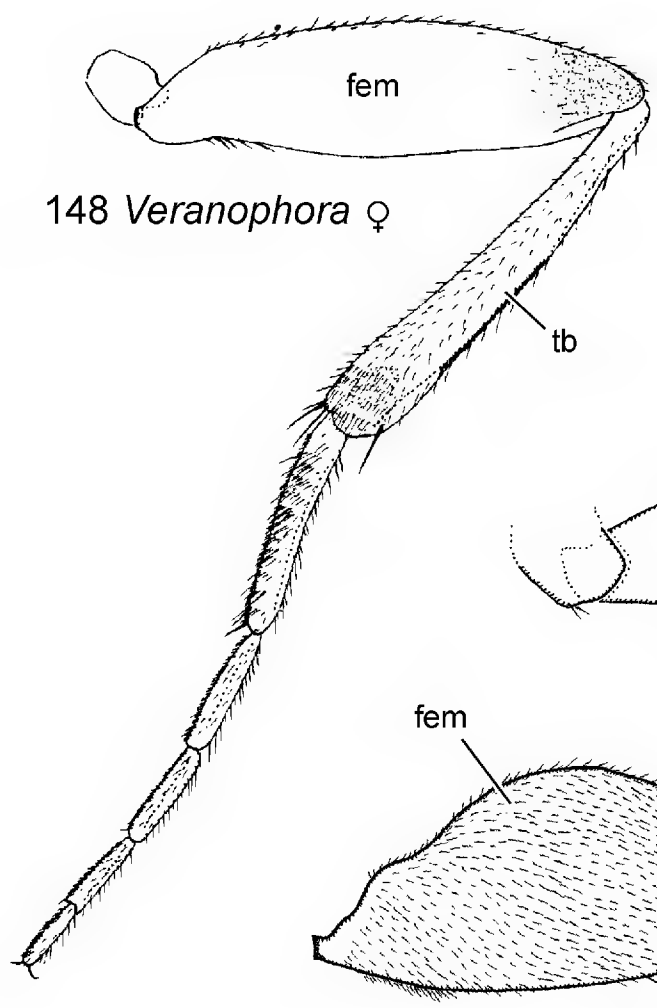
Figs 59.140–147. Mid and hind legs and leg features of Phoridae: (140) mid leg of *Linklloydia ivorensis* (Delachambre), anterior view ♀; (141) mid femur of *Conicera tibialis* Schmitz, posterior view ♂; (142) same, mid tibia, anterior view ♂; (143) same, *Thaumatoxena andreinii* Silvestri ♀; (144) hind leg of *Aenictacantha setifera* Disney, anterior view ♀; (145) same, *L. ivorensis*, anterior view ♀; (146) same, sighted female morph of *Metopina ciceri* Disney, posterior view ♀; (147) mid femur of *Th. andreinii*, anterior view ♀. Figs 140, 145 (Disney & Kistner 1995, figs 10, 9, respectively), Fig. 141 (Disney 1983*b*, fig. 38), Fig. 142 (Disney *et al*. 2010, fig. 6D), Fig. 143 (Disney & Kistner 1992, fig. 34), Figs 144, 146 (Disney 1994, figs 8.19a, 1.3a, respectively), Fig. 147 (Disney & Kistner 1992, fig. 32).

Abbreviations: fem – femur; s – seta; tb – tibia.

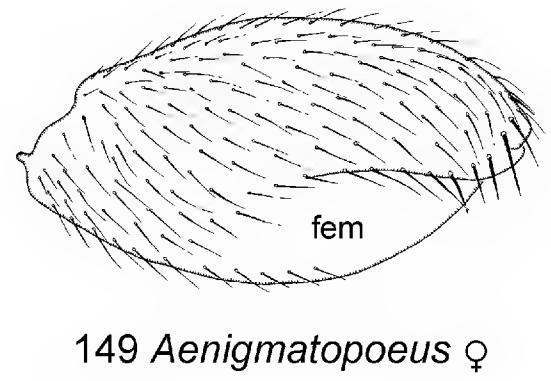
[***Latiborophaga* Brown**. See *Borophaga*].

***Linklloydia* Disney** (Phorinae: Termitoxeniini)**.** An endemic monotypic genus, with the single species, *L. ivorensis*, only known from the female, described from Côte d'Ivoire. Adults occur in colonies of the termite *Protermes prorepens*, but the immature stages remain unknown. The species was treated by Disney & Kistner (1995).

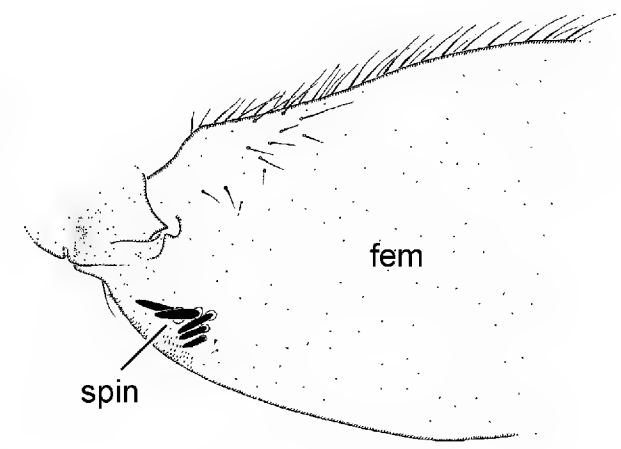
***Macrocerides* Borgmeier** (Metopininae)**.** A genus of nine species, occurring in the Afrotropical and Neotropical Regions. Borgmeier (1969: 69) remarked that "This genus is rather heterogeneous. It is quite possible that some species … do not belong". Brown (2011) endorsed this opinion and re-assigned some species to a separate genus. All but the single Afrotropical species are Neotropical. Brown (2011) considered it unlikely that the single Afrotropical species, *Ma. leydheckeri*



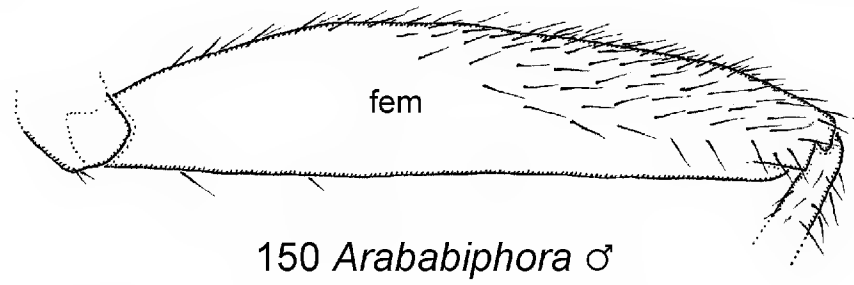
148 *Veranophora* ♀



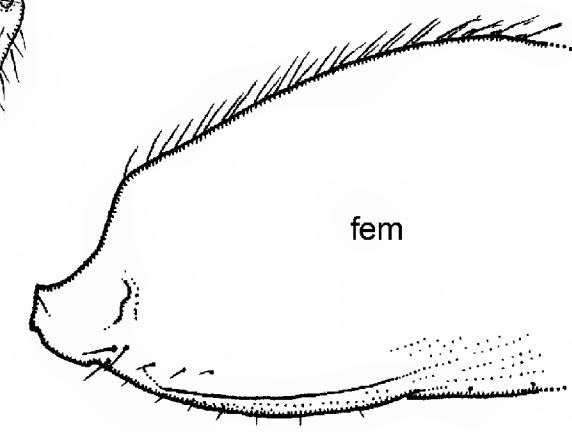
149 *Aenigmatopoeus* ♀



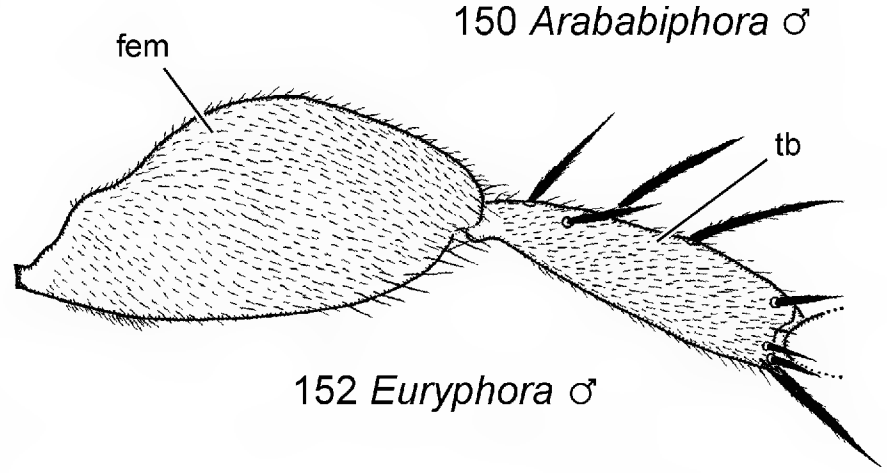
151 *Dohrniphora* ♂



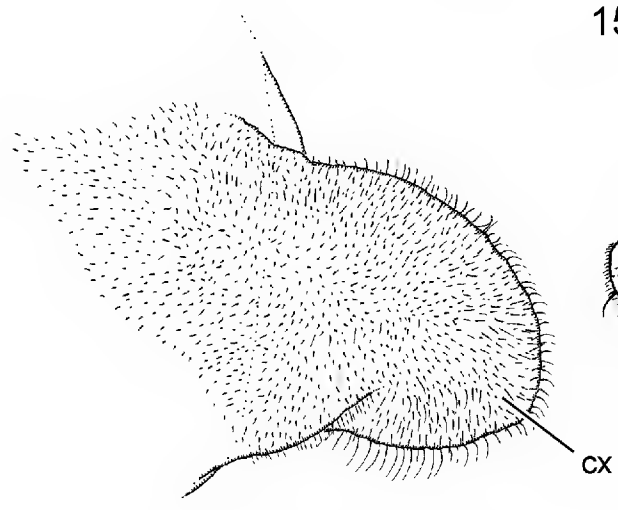
150 *Arababiphora* ♂



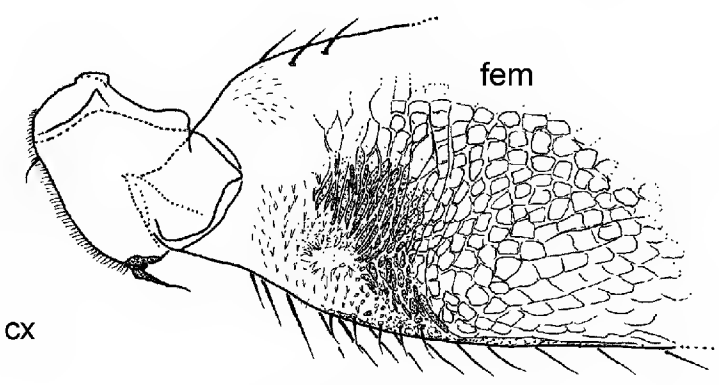
153 *Gymnoptera* ♂



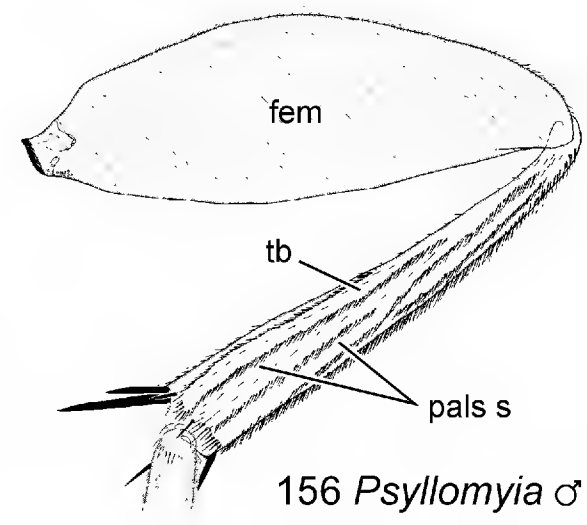
152 *Euryphora* ♂



154 *Dohrniphora* ♂



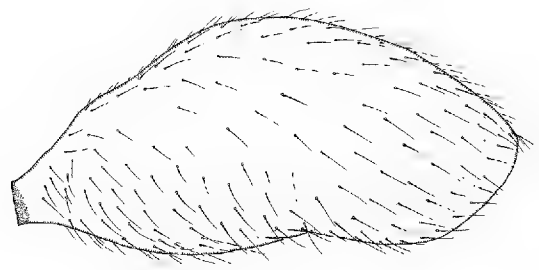
155 *Metopina* ♂



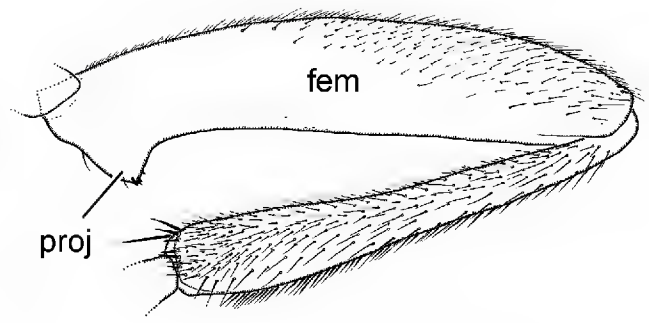
156 *Psyllomyia* ♂

Figs 59.148–156. Hind legs and leg features of Phoridae: (148) hind leg of *Veranophora medleri* (Disney), posterior view ♀; (149) hind femur of *Aenigmatopoeus kohli* Schmitz, anterior view ♀; (150) same, *Arabiphora tenuifemorata* Disney, posterior view ♂; (151) base of hind femur of *Dohrniphora cornuta* (Bigot *in* de la Sagra) ♂; (152) hind femur and tibia of *Euryphora arabiensis* Disney, anterior view ♂; (153) base of hind femur of *Gymnoptera simplex* (Brues), posterior view ♂; (154) hind coxal lobe of *D. cornuta*, lateral view ♂; (155) male hind trochanter and base of femur of *Metopina heselhausi* Schmitz, posterior view ♂; (156) hind femur and tibia of *Psyllomyia braunsi* Schmitz, left lateral view ♂. Figs 148, 150, 152, 154, 155 (Disney 2006, figs 118, 7, 42, 33, 51, respectively), Fig. 151 (Disney 1994, fig. 6.12b), Fig. 153 (Disney 2003e, fig. 5), Fig. 156 (Disney 1979c, fig. 3, as *Multinevra*).

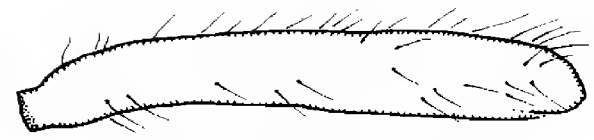
Abbreviations: cx – coxa; fem – femur; pals s – palisade setae; spin – spinules; tb – tibia.



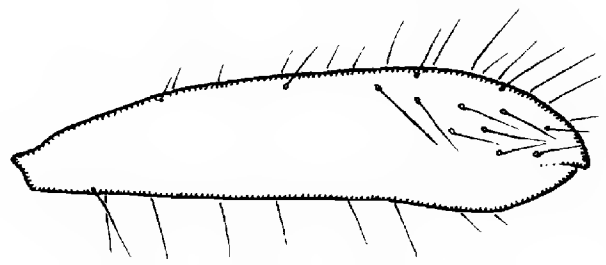
157 *Psyllomyia* ♀



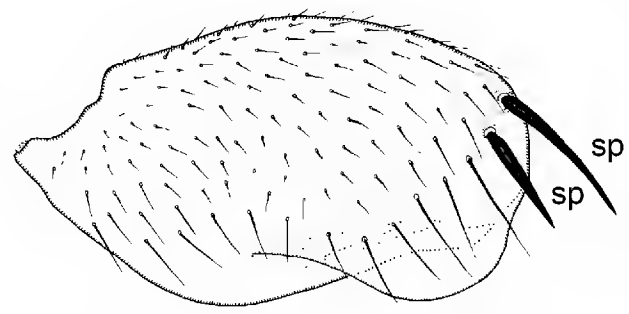
162 *Razorfemora* ♂



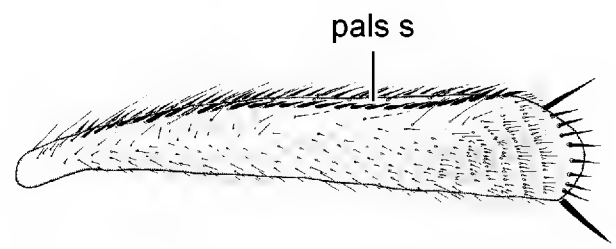
167 *Termitophilomyia* ♂



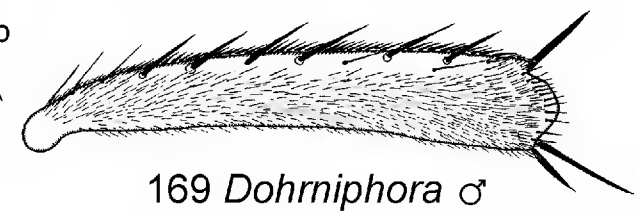
158 *Termitophilomyia* ♀



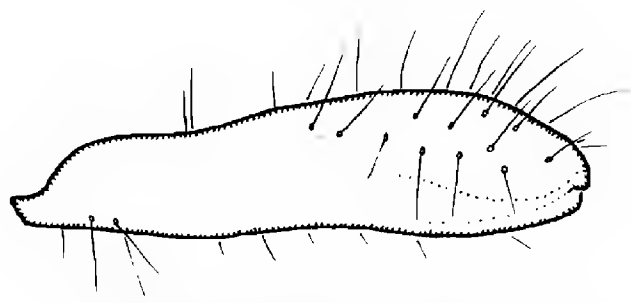
163 *Thaumatoxena* ♀



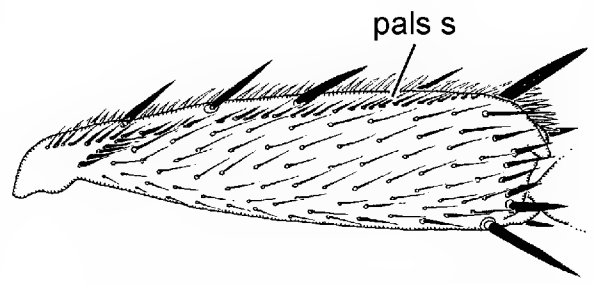
168 *Diplonevra* ♂



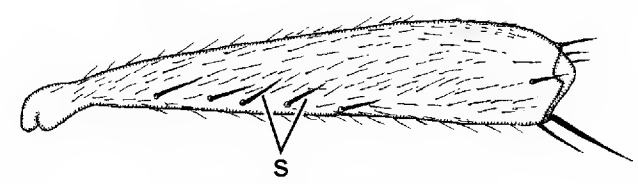
169 *Dohrniphora* ♂



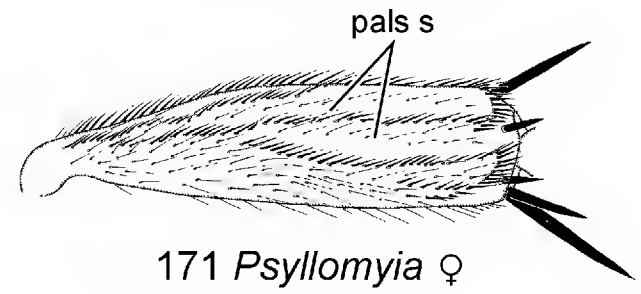
159 *Termitophilomyia* ♀



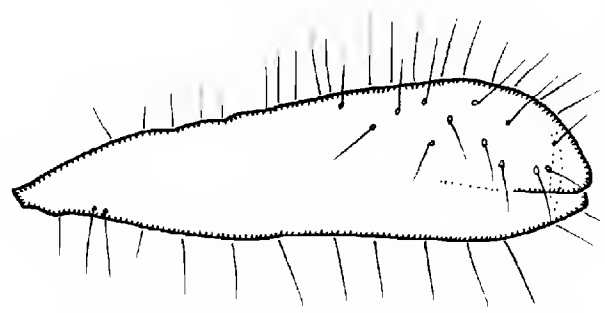
164 *Aenigmatopoeus* ♀



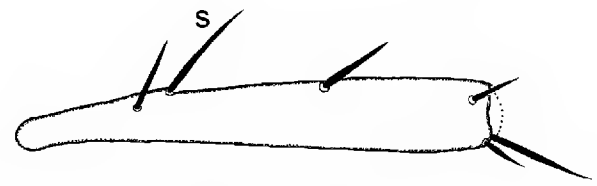
170 *Phlebothrix* ♀



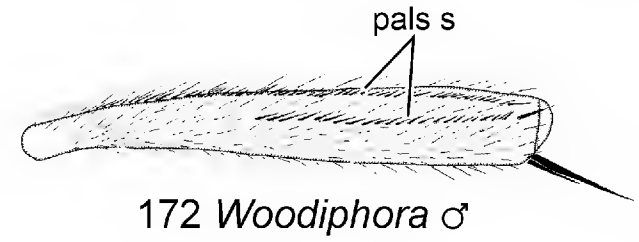
171 *Psyllomyia* ♀



160 *Termitophilomyia* ♀

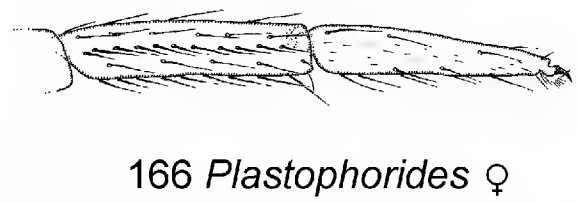


165 *Conicera* ♀

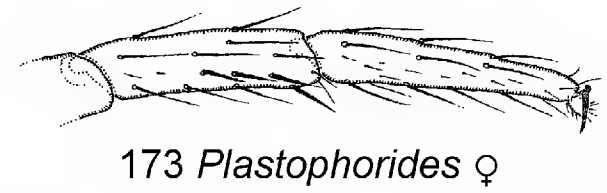


172 *Woodiphora* ♂

161 *Metopina* ♂



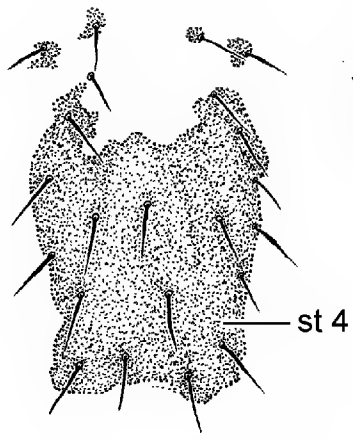
166 *Plastophorides* ♀



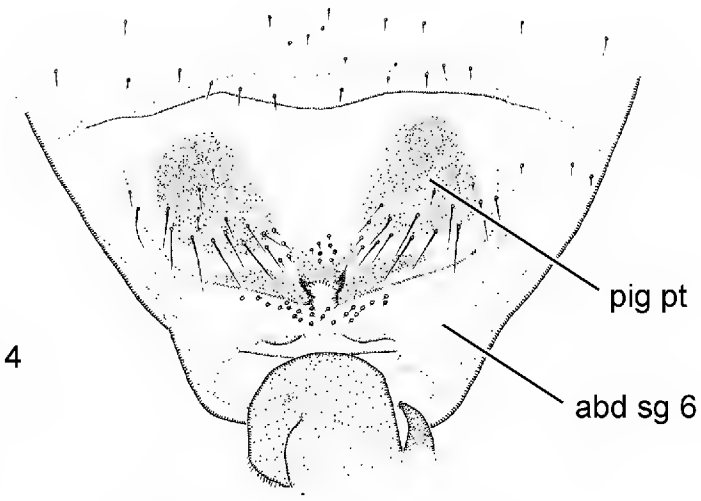
173 *Plastophorides* ♀

Figs 59.157–173. Hind legs and leg features of Phoridae: (157) hind femur of *Psyllomyia braunsi* Schmitz, anterior view ♀; (158) hind femur of *Termitophilomyia zimbraunsi* Disney (flying stage), posterior view ♀; (159) same (flightless stenogastric stage); (160) same (flightless physogastric stage); (161) hind tibia and tarsomere 1 of *Metopina ciceri* Disney, posterior view ♂; (162) hind femur and tibia of *Razorfemora nussbaumi* Disney, posterior view ♂; (163) hind femora of *Thaumatoxena andreinii* Silvestri, anterior view ♀; (164) hind tibia of *Aenigmatopoeus kohli* Schmitz, anterior view ♀; (165) same, *Conicera tibialis* Schmitz (setulae omitted); (166) hind tarsomeres 4 and 5 of *Plastophorides aculeipes* (Collin), lateral view ♀; (167) hind femur of *T. zimbraunsi* (flightless physogastric stage), anterior view ♂; (168) hind tibia of *Diplonevra* sp., posterior view ♂; (169) same, *Dohrniphora isopterorum* Disney; (170) same, *Phlebothrix cochleariparpis* (Speiser), anterior view ♀; (171) same, *Ps. braunsi*; (172) same, *Woodiphora collini* Disney ♂; (173) hind tarsomeres 4 and 5 of *Plastophorides aculeipes*, lateral view ♀. Fig. 157 (Disney 2006, fig. 78), Figs 158–160 (Disney & Kistner 1995, fig. 112), Fig. 161 (Disney 1988, fig. 6), Fig. 162 (Disney 1994, fig. 8.78c), Figs 166–168, 171, 173 (Disney 1994, figs 8.72c, 8.85d, 8.39f, 8.60c, 8.72d, respectively), Fig. 163 (Disney & Kistner 1992, fig. 31), Fig. 165 (Disney 1983*b*, fig. 42), Fig. 169 (Disney & Darlington 2000*a*, fig. 2), Figs 170, 172 (Disney 2009*b*, figs 154, 178).

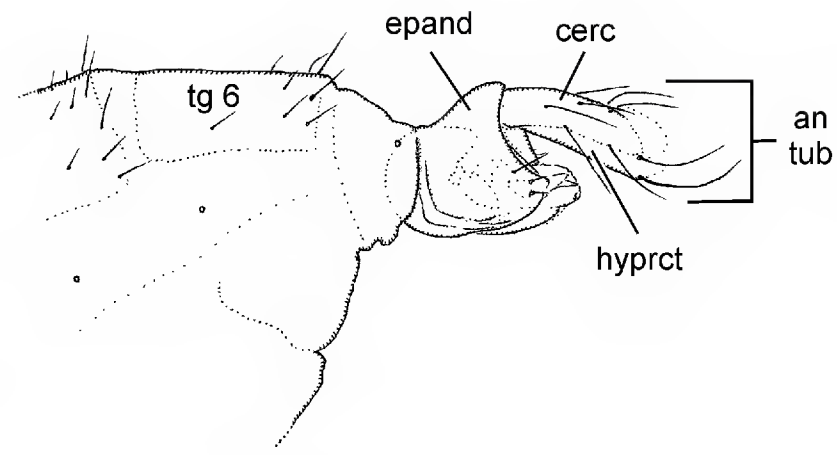
Abbreviations: cten – ctenidia; fem – femur; pals s – palisade setae; proj – projection; s – seta(e); sp – spine.



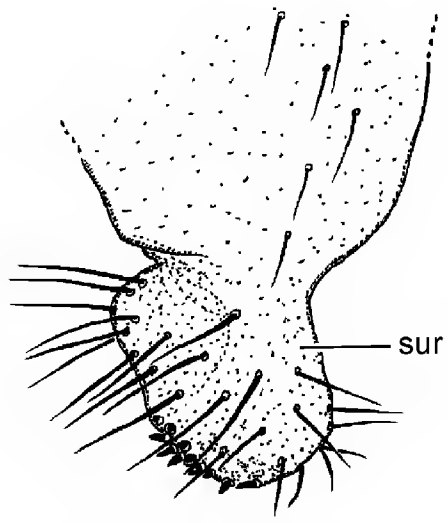
174 *Metopina* ♂



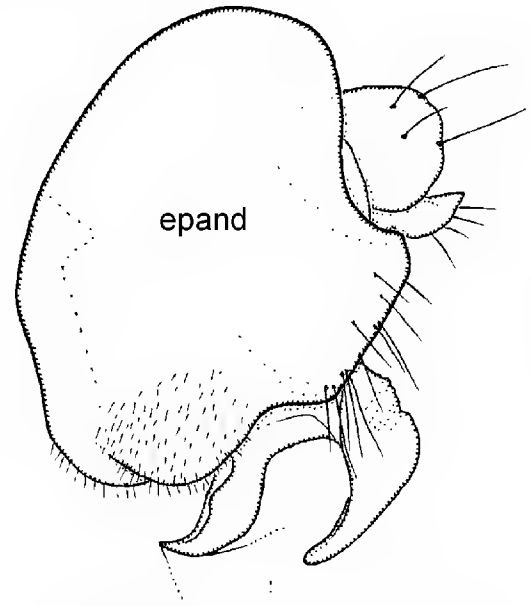
175 *Plastophorides* ♂



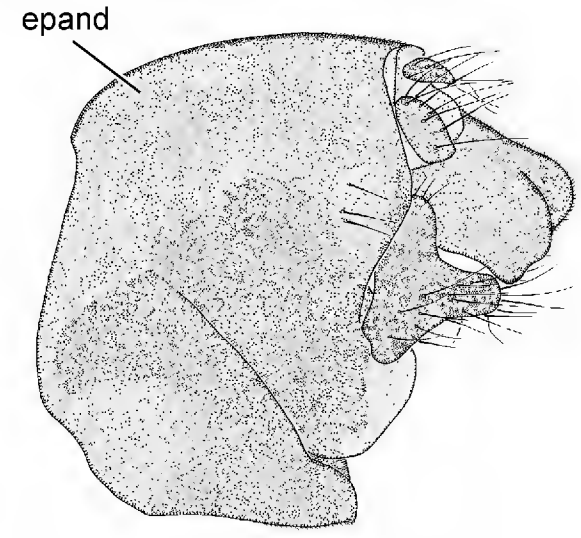
176 *Arababiphora* ♂



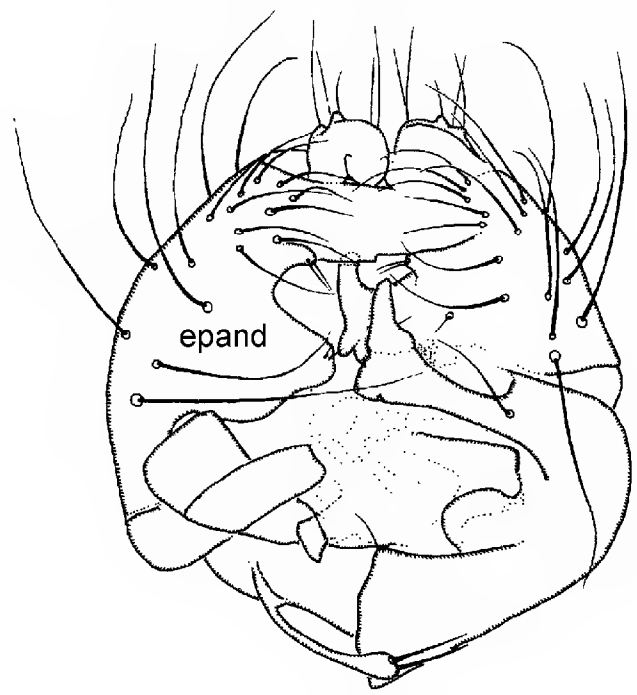
177 *Conicera* ♂



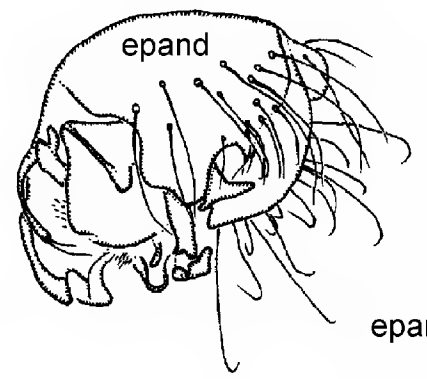
178 *Aenigmatistes* ♂



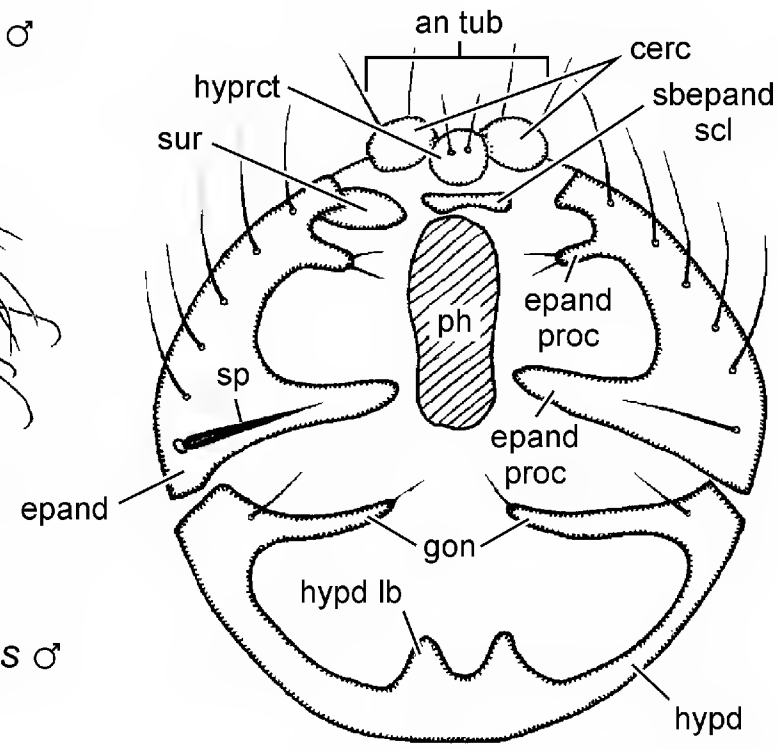
179 *Beyermyia* ♂



180 *Chonocephalus* ♂



181 *Chonocephalus* ♂

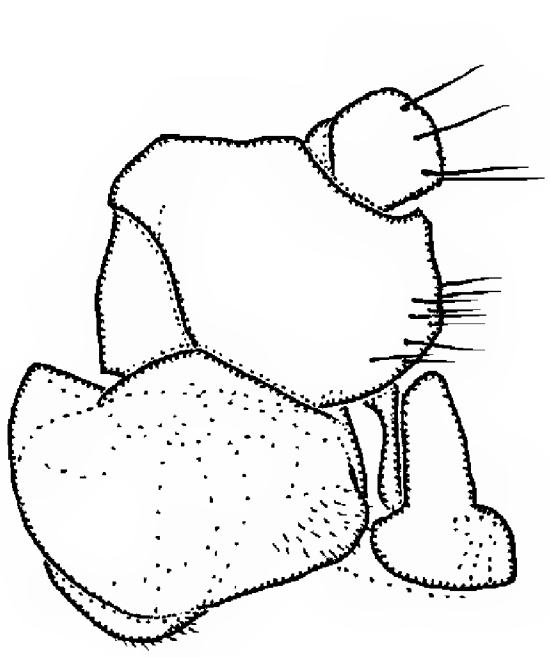


182 *Chonocephalus* ♂

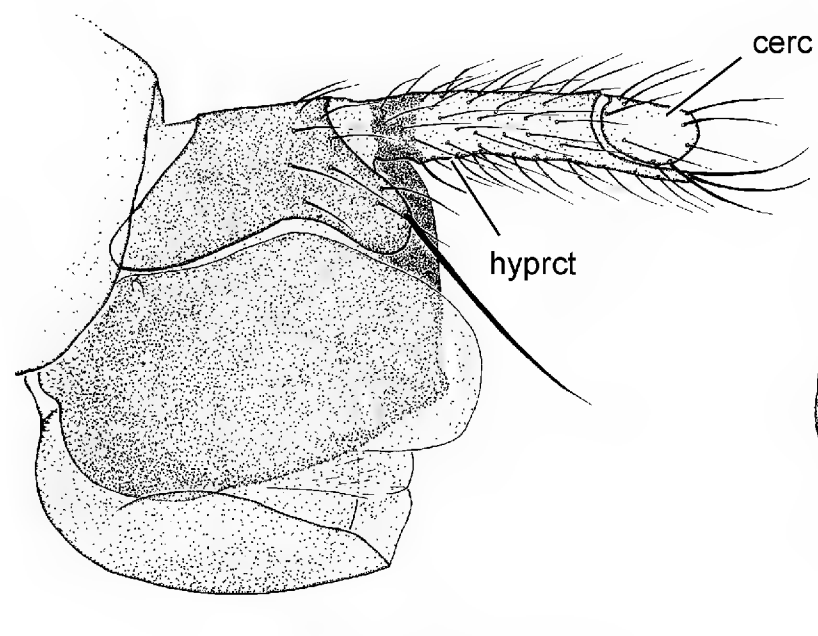
Figs 59.174–182. Male abdominal features and terminalia of Phoridae: (174) abdominal sternite 4 of *Metopina heselhausi* Schmitz, ventral view; (175) abdominal segment 6 of *Plastophorides aculeipes* (Collin), ventral view; (176) tergite 6 and hypopygium of *Arabiphora tenuifemorata* Disney, lateral view; (177) surstylus of male hypopygium of *Conicera tibialis* Schmitz, right lateral view; (178) hypopygium of *Aenigmatistes scutellatus* (Becker), left lateral view; (179) same, *Beyermyia spinulicosta* (Beyer); (180) same, *Chonocephalus heymonsi* Strobbe, ventral view; (181) same, left lateral view; (182) same, *Chonocephalus* sp., ventral view. Figs 174, 176, 178, 182 (Disney 2006, figs 50, 8, 4, 11, respectively), Figs 175, 179–181 (Disney 1994, figs 8.71b, 8.10b, 8.30a, 8.30b, respectively), Fig. 177 (Disney 1983*b*, fig. 33).

Abbreviations: abd sg – abdominal segment; an tub – anal tube; cerc – cercus; epand – epandrium; epand proc – epandrial process; gon – gonopod; hypd – hypandrium; hypd lb – hypandrial lobe; hyprct – hypoproct; ph – phallus; pig pt– pigmentation patch; sbepand scl – subepandrial sclerite; sp – spine; sur – surstylus; st – sternite; tg – tergite.

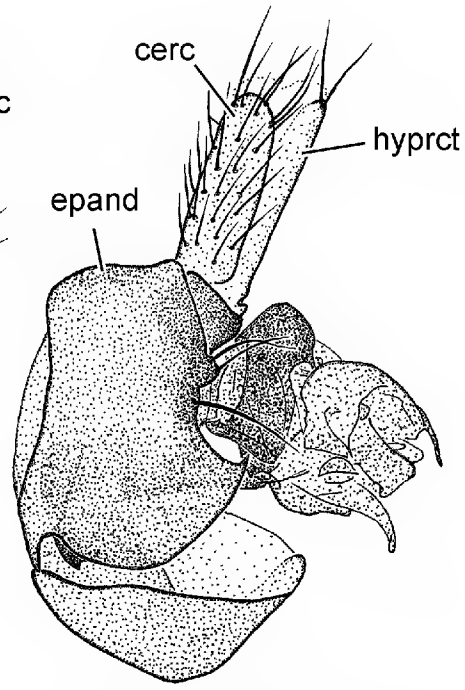
(*sensu* Schmitz *in* Beyer, 1965 and Borgmeier (1969)), described from Democratic Republic of Congo, is congeneric with the Neotropical species. Indeed, it is only distinguishable from the genus *Megaselia* (by both Beyer and Borgmeier), on the basis of the elongate postpedicel. It seems quite probable that this species is the male of *Megaselia ctenophora* Beyer, 1965, which is only known in the female sex. If this proves to be the case, then *Ma. leydheckeri* would become a synonym



183 *Danumphora* ♂

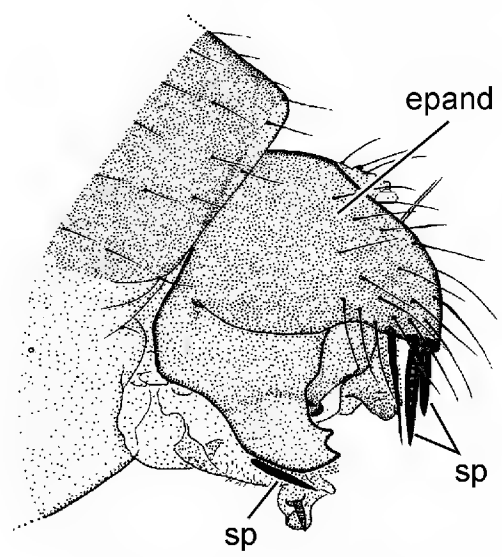


184 *Diplonevra* ♂

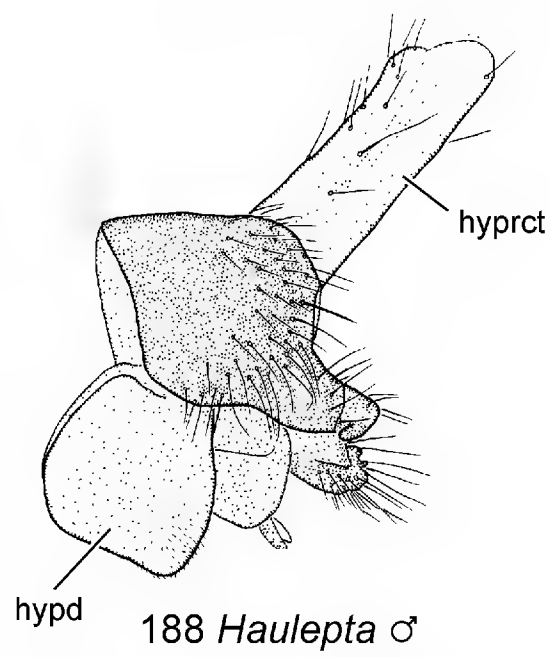


185 *Dohrniphora* ♂

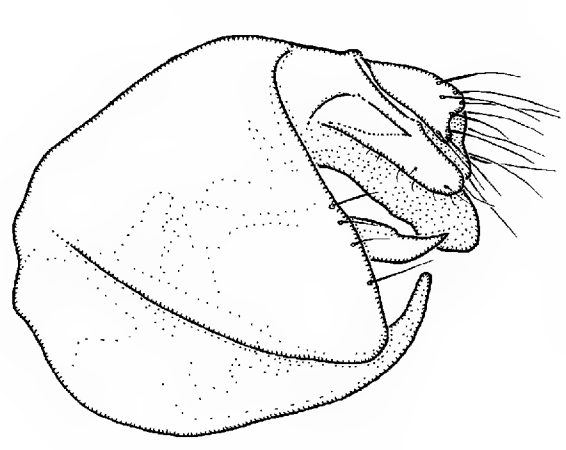
186 *Euryphora* ♂



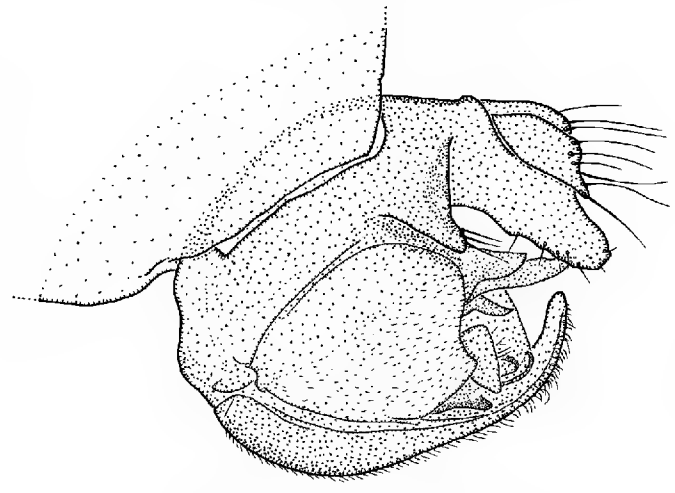
187 *Gymnoptera* ♂



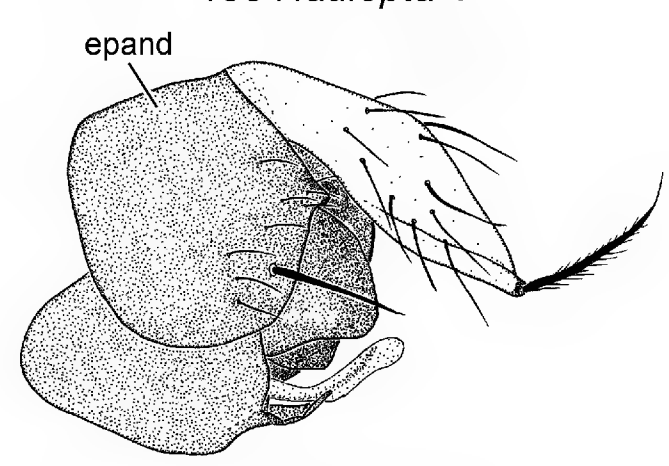
188 *Haulepta* ♂



189 *Hypocerides* ♂



190 *Hypocerides* ♂



191 *Megaselia* ♂

Figs 59.183–191. Male terminalia (hypopygia) of Phoridae (lateral views, unless otherwise stated): (183) *Danumphora hageri* Disney, left lateral view; (184) *Diplonevra* sp.; (185) *Dohrniphora cornuta* (Bigot *in* de la Sagra); (186) *Euryphora arabiensis* Disney; (187) *Gymnoptera simplex* (Brues); (188) *Haulepta sheasbyi* Disney; (189) *Hypocerides nearcticus* Borgmeier, right lateral view; (190) same, left lateral view; (191) *Megaselia scalaris* Loew. Figs 183, 186, 189, 190 (Disney 2006, figs 29, 43, 46, 48), Figs 184, 185 (Disney 1994, figs 8.13b, 8.12c, respectively), Fig. 187 (Disney 2003e, fig. 6), Fig. 188 (Disney & Kistner 1997, fig. 10), Fig. 191 (Disney 1991c, 40).

Abbreviations: cerc – cercus; epand – epandrium; hypd – hypandrium; hyprct – hypoproct; sp – spine(s).

of *Me. ctenophora* and the genus *Macrocerides* would cease to be recorded as Afrotropical. Biology and immature stages remain unknown.

***Mannheimsia* Beyer** (Phorinae)**.** A genus of six described species, occurring in the Afrotropical, Neotropical and Oriental Regions. The single Afrotropical species, *M. sticta* Beyer, 1965, is recorded from Democratic Republic of Congo, Kenya and Nigeria. Biology and immature stages remain unknown. This species was also treated by Ament (2012).

***Megaselia* Rondani** (Metopininae: Gymnophorini)**.** A genus of more than 1,400 described species, occurring in all zoogeographical regions, including Antarctica and representing at least half of the described Phoridae globally. At least 230 species occur in the Afrotropical Region, but probably ten times that number remain undescribed. Species recognition is currently based on the male sex in the first instance. Undescribed females should be given code letters or numbers until linked to respective males. It is here emphasised that undescribed species are likely to be encountered in almost any collection of Phoridae. Meunier (1905, 1910) was the first to describe *Megaselia* species from the Afrotropics, albeit from subfossil resins (copal) from different parts of the continent. Beyer (1965) provided identification keys to Afrotropical species, but these are seriously flawed by errors and omissions and by runs of couplets based on males, followed by runs based on females alone, before returning to runs based on males alone. Males and females should be keyed separately, as has been done in preliminary treatments for parts of the region other than the continental Afrotropics. These are for: Cabo Verde (Disney 1991*c*); Madagascar and adjacent islands (Disney 2005*e*); Seychelles (Disney 2009*b*); and the Arabian Peninsula (Disney 2009*c*). Many included species in these works also occur in the continental Afrotropics. Species in genera subsequently synonymised with *Megaselia* also need to be considered (Colyer & Elberg 1969; Disney 1990*a*, Disney & Kistner 1997). A species assigned to "*Pericyclocera*" by Schmitz (1940), for example, runs to couplet 7 at the top of page 51 of Beyer's (1965) identification key. *Megaselia* is the genus of insects with a greater diversity of larval habits than any other family of insects. These habits include feeders on micro-organisms in aquatic (container) habitats, dung- and carrion-breeders (including human corpses), fungivores, plant-feeders, predators, parasitoids and parasites (see Disney 1994, for review). For species identification for the continental Afrotropics Bridarolli's (1951) pioneering paper is still a useful companion (especially for the photographs of wings), to Beyer's (1965) monograph. Additional species are covered by Borgmeier (1967), Compton & Disney (1991), Disney (1978, 1982*b*, 1985*a*, 1989*a*, 1991*a*, *b*, 2004*a*, *c*), Disney & Kistner (1997, 1998, 2003), Disney *et al.* (2013*a*), Mostovski (2015) and Srivathsan *et al.* (2019).

***Menozziola* Schmitz** (Metopininae: Gymnophorini)**.** A genus of nine species occurring in the Afrotropical and Neotropical Regions and Holarctic Realm, but whether all nine species truly belong to a single genus remains in question. Two species occur in the Afrotropics, *M. fraterna* Beyer, 1965 and *M. sororia* Beyer, 1965, both being described from Democratic Republic of Congo. *Menozziola* are known to parasitise ants of the genus *Camponotus*, but the immature stages remain unknown. An identification key to the two Afrotropical species is currently unavailable.

***Metopina* Macquart** (Metopininae: Metopinini)**.** A genus of more than 30 described and numerous undescribed species, occurring in all zoogeographical regions, except Antarctica. A single continental Afrotropical species, *M. obsoleta*, recorded from Uganda and Zimbabwe, was re-described by Disney & Kistner (1989) and three species: *M. heselhausi* Schmitz, 1914; *M. vanharteni* Disney, 2006 and *M. ventralis* Schmitz, 1927, were recorded from Yemen, in the Southern Arabian Peninsula and were keyed by Disney (2006: 495), one of which has subsequently been recorded from Benin in West Africa (Disney *et al.* 2013*a*). Confusion has been caused by previous authors naming species on the basis of a single sex and modern descriptions should be based on both sexes or on females alone. Undescribed males should be given code letters or numbers until linked to their respective females. Other undescribed species are known from the region. The larvae of extralimital species are recorded as inhabiting the root nodules of Chickpeas (Disney 1988) and are expected to occur in the Afrotropical Region. *Metopina heselhausi* was reared from a fungus *Russula* species (Russulaceae) (Disney *et al.* 2013*a*), otherwise biology and immature stages remain unknown.

***Miclepta* Disney** (Metopininae)**.** An endemic monotypic genus, with the single species, *M. arrujumensis* Disney, 2006, known from the female only, described from Yemen in the Southern Arabian Peninsula. Biology and immature stages remain unknown. The species was treated by Disney (2006: 499).

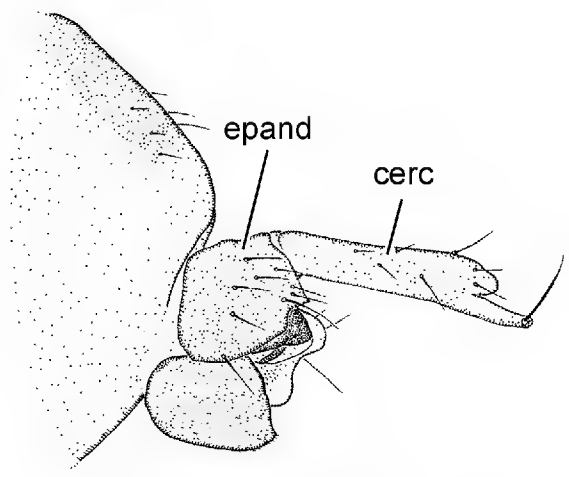
***Microplatyphora* Schmitz** (Phorinae: Aenigmatiini)**.** An endemic monotypic genus with the single species, *M. congolensis* Schmitz, 1915, known from the female only, described from Democratic Republic of Congo. Adults are recorded from colonies of the ant *Tetramorium aculeatum*, but the immature stages remain unknown.

***Microselia* Schmitz** (Metopininae: Gymnophorini)**.** A genus of thirteen species, occurring in the Afrotropical, Oriental and Palaearctic Regions and Holarctic Realm. Six species occur in the Afrotropics, distributed in Central, Southern and West Africa and in Yemen in the Southern Arabian Peninsula. The genus is poorly known and at least one species is probably misclassified. Species recognitions is based on the female sex in the first instance. The holotype of *M. deemingi* was caught hovering over a worker, suggesting the genus is probably myrmecophilous, but the biology and immature stages otherwise remain unknown. The six Afrotropical species were treated by Disney (1983*a*, 1991*a*, 2006: 500).

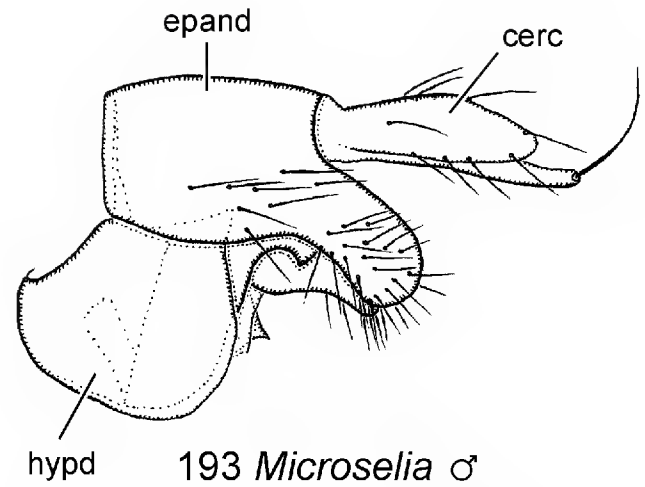
***Morahania* Schmitz** (Metopininae)**.** An endemic monotypic genus with the single species, *M. palliata* Schmitz, 1958, known only from the female sex, described from Angola and Democratic Republic of Congo (Schmitz 1958). Biology and immature stages remain unknown.

***Necperissa* Disney** (Phorinae: Termitoxeniini)**.** An endemic monotypic genus with the single species, *N. tinglei*, described from Tanzania and Zimbabwe. Adults are recorded in colonies of the termite *Odontotermes lacustris*, but the immature stages remain unknown. The species was treated by Disney & Kistner (1995).

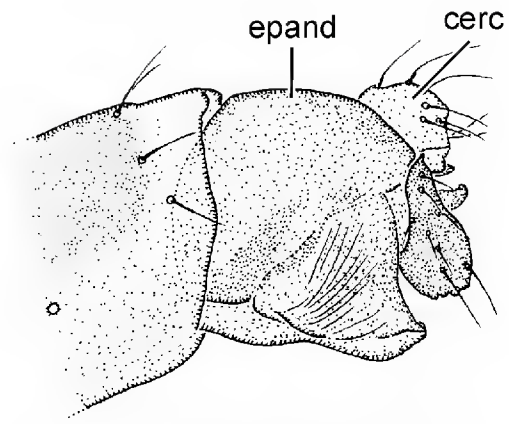
***Paratermitoxenia* Beyer** (Phorinae: Termitoxeniini)**.** An endemic monotypic genus with the single species, *P. coatoni*,



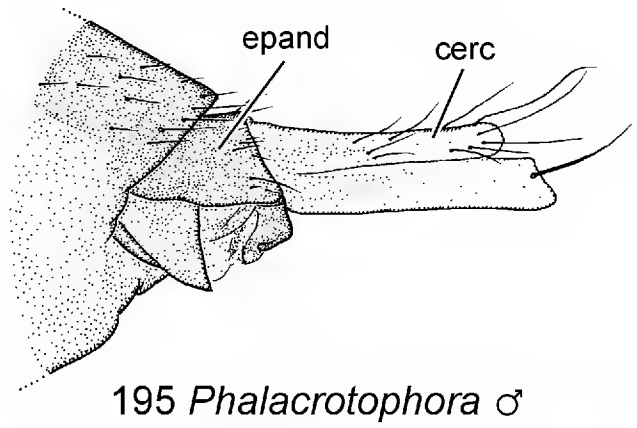
192 *Menozziola* ♂



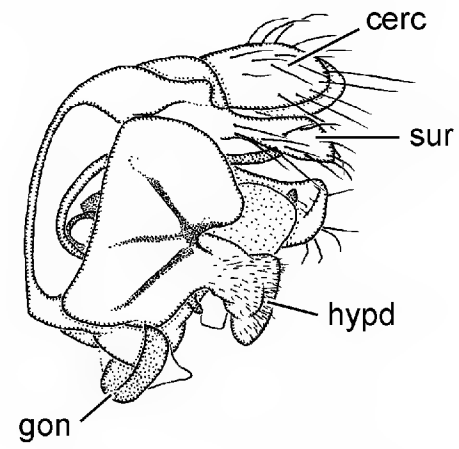
193 *Microselia* ♂



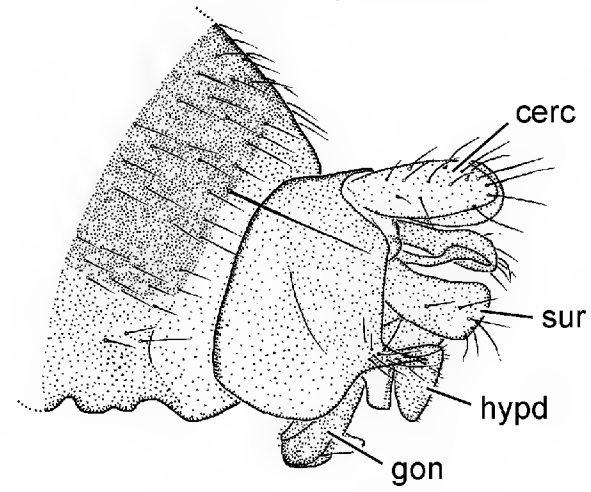
194 *Necperissa* ♂



195 *Phalacrotophora* ♂

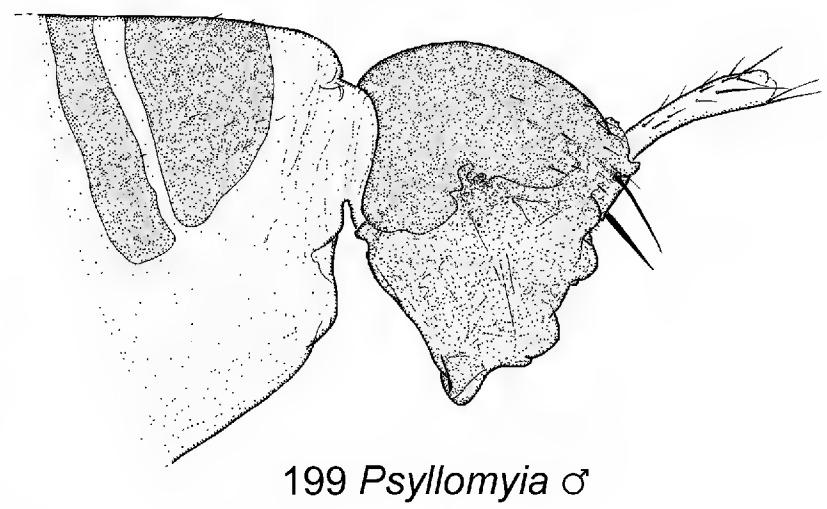


196 *Phlebothrix* ♂

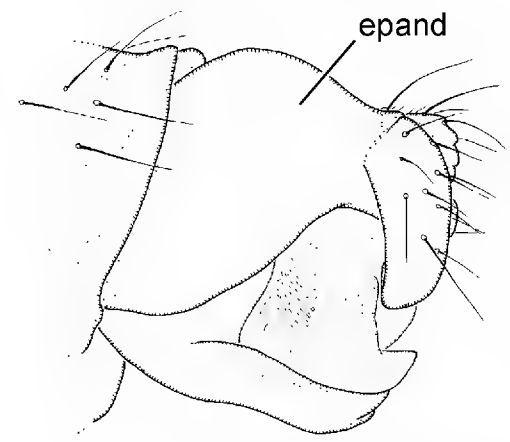


197 *Phlebothrix* ♂

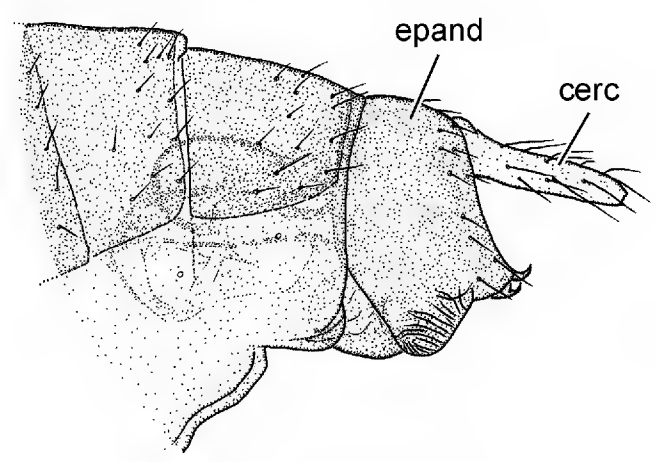
198 *Plethysmochaeta* ♂



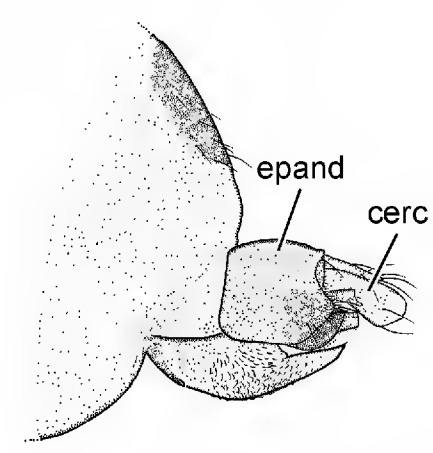
199 *Psyllomyia* ♂



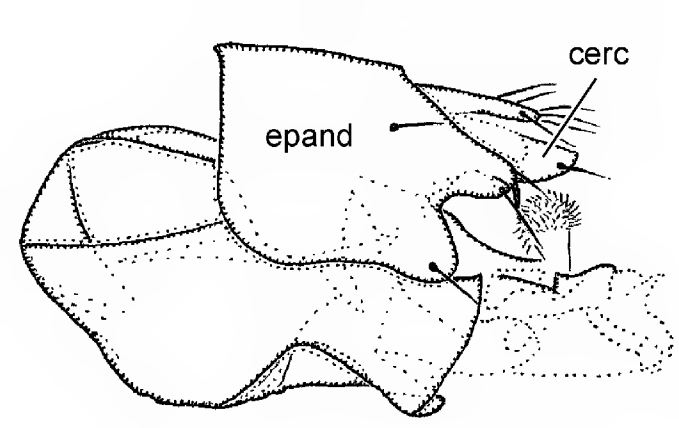
200 *Ptochomyia* ♂



201 *Puliciphora* ♂



202 *Puliciphora* ♂



203 *Puliciphora* ♂

Figs 59.192–203. Male terminalia (hypopygia) of Phoridae (lateral views, unless otherwise stated): (192) *Menozziola schmitzi* (Menozzi) (non-Afrotropical); (193) *Microselia yemenensis* Disney; (194) *Necperissa tinglei* (Disney); (195) *Phalacrotophora occidentata* (Disney); (196) *Phlebothrix cochlearipalpis* (Speiser), right lateroventral view; (197) same, left laterodorsal view; (198) *Plethysmochaeta trinervis* (Schmitz); (199) *Psyllomyia braunsi* Schmitz; (200) *Ptochomyia cummingae* Disney; (201) *Puliciphora borinquenensis* Wheeler; (202) *Pu. pulex* Dahl; (203) *Pu. imitata* Disney. Fig. 192 (Gadau & Disney, 1996, fig. 2), Figs 193, 195 (Disney 2006, figs 72, 130, as *Zygtaxphora*), Fig. 194 (Disney 1994, fig. 8.69a), Figs 196, 201, 202 (Disney 2009*b*, figs 151, 166, 171), Fig. 197 (Disney 2005e, fig. 3), Fig. 198 (Disney 1995*b*, fig. 3), Fig. 199 (Disney & Kistner 1998, fig. 20), Fig. 200 (Disney & Kistner 1995, fig. 39), Fig. 203 (Disney 2008*b*, fig. 112).

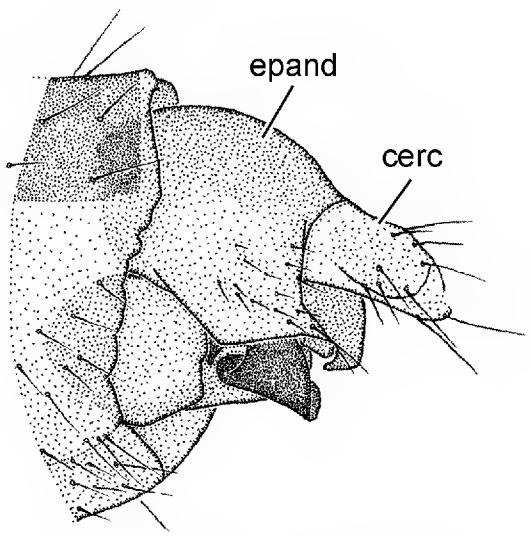
Abbreviations: cerc – cercus; epand – epandrium; gon – gonopod; hypd – hypandrium; sur – surstylus.

known from the female only, described from South Africa. Adults are recorded in colonies of the termite *Allodontotermes rhodesiensis*, but the immature stages remain unknown. The species was treated by Disney & Kistner (1995).

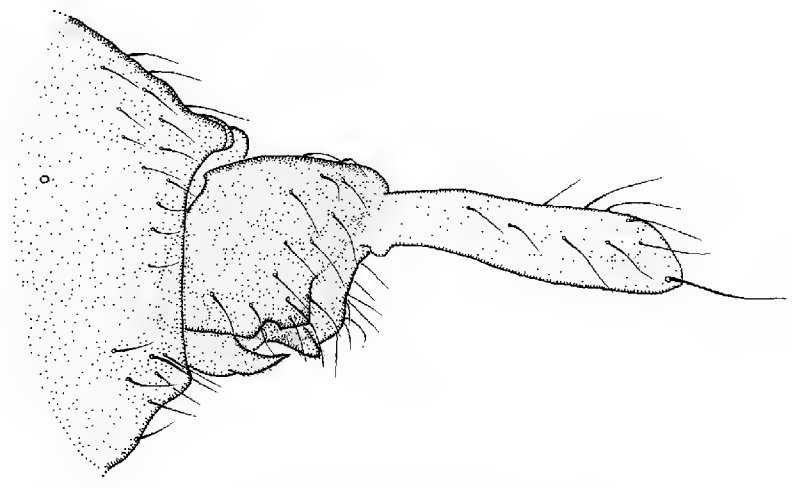
***Penthaplus* Schmitz** (Metopininae)**.** An endemic monotypic genus with the single species, *P. exilis* Schmitz, 1958, described from Angola. Biology and immature stages remain unknown.

***Perittophora* Disney** (Phorinae: Termitoxeniini)**.** An endemic monotypic genus with the single species, *P. couturieri* Disney, 1990, known only from the female described from Zimbabwe. Biology and immature stages remain unknown. The species was treated by Disney & Kistner (1995).

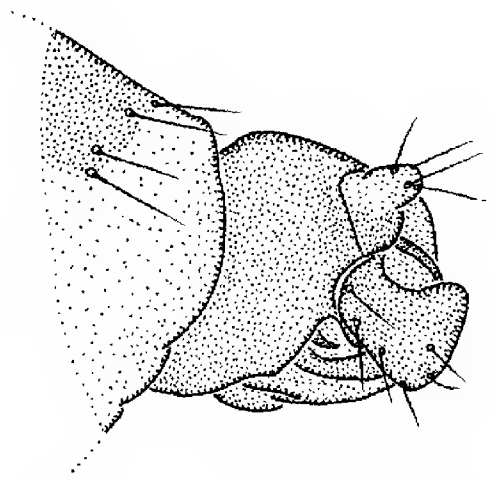
***Phalacrotophora* Enderlein** (Metopininae: Gymnophorini)**.** A genus of *ca* 50 species occurring in all zoogeographical



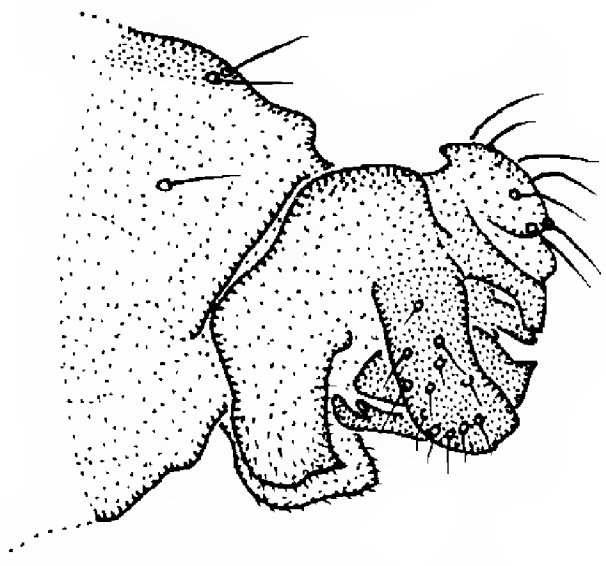
204 *Razorfemora* ♂



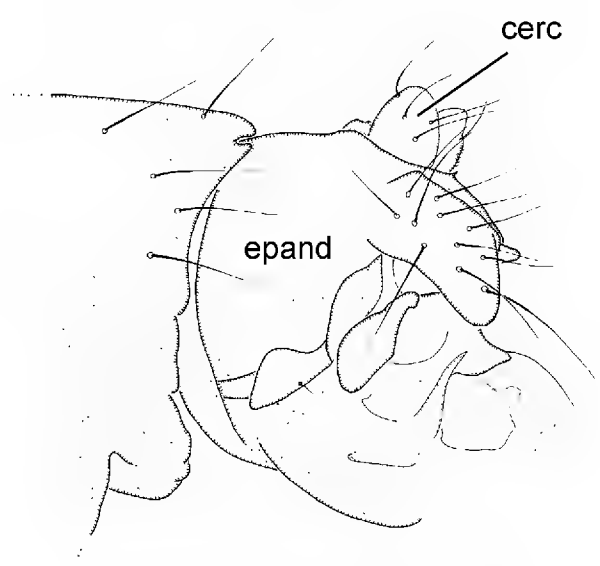
205 *Ritchiephora* ♂



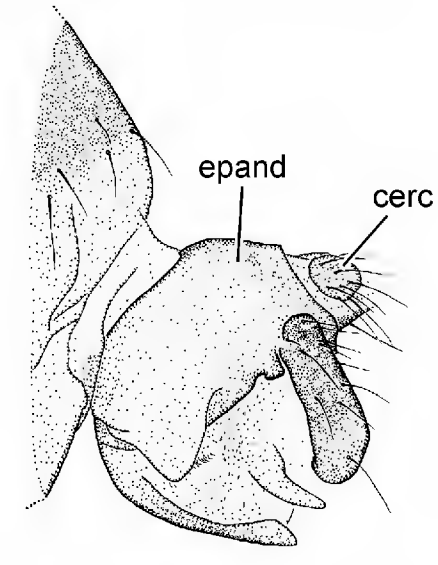
206 *Syntermitoxenia* ♂



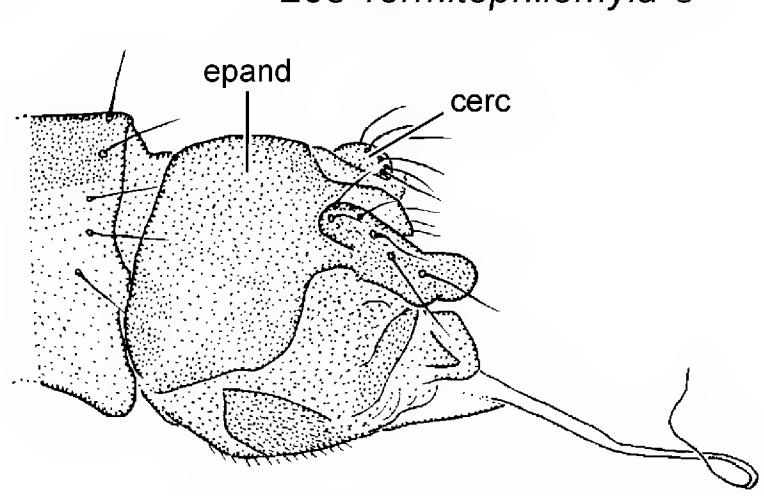
207 *Syntermitoxenia* ♂



208 *Termitophilomyia* ♂



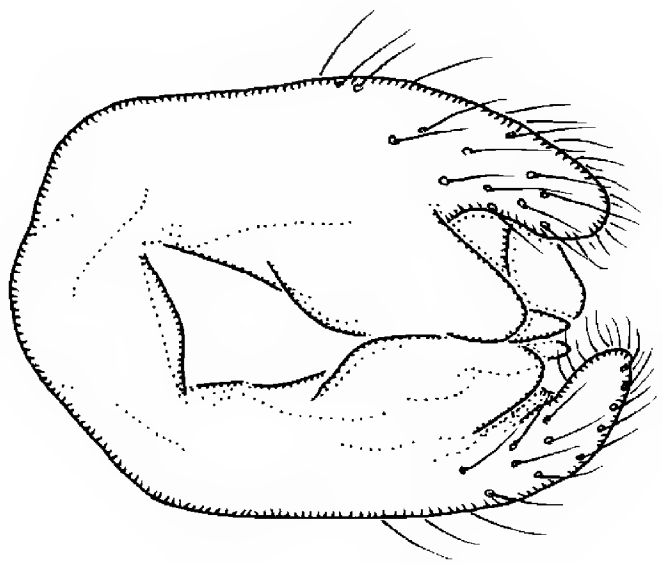
209 *Termitosagma* ♂



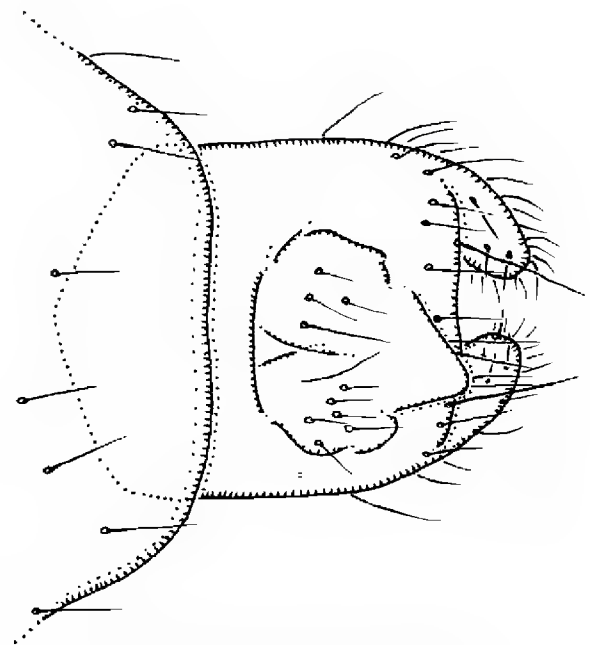
210 *Termitoxenia* ♂

Figs 59.204–210. Male terminalia (hypopygia) of Phoridae (lateral views): (204) *Razorfemora nussbaumi* Disney; (205) *Ritchiephora diplopodae* Disney; (206) *Syntermitoxenia jaegerskioeldi* (Wasmann); (207) *S. lewisi* (Disney); (208) *Termitophilomyia zimbraunsi* Disney; (209) *Termitosagma henningsi* Reichensperger; (210) *Termitoxenia oligoseta* (Disney). Fig. 204 (Disney 2006, fig. 87), Fig. 205 (Disney & Ritchie 1997, fig. 3), Figs 206, 207, 210 (Disney 1994, figs 8.82b, 8.82c), Fig. 208 (Disney & Kistner 1995, fig. 113), Fig. 209 (Disney & Darlington 2000a, fig. 10).

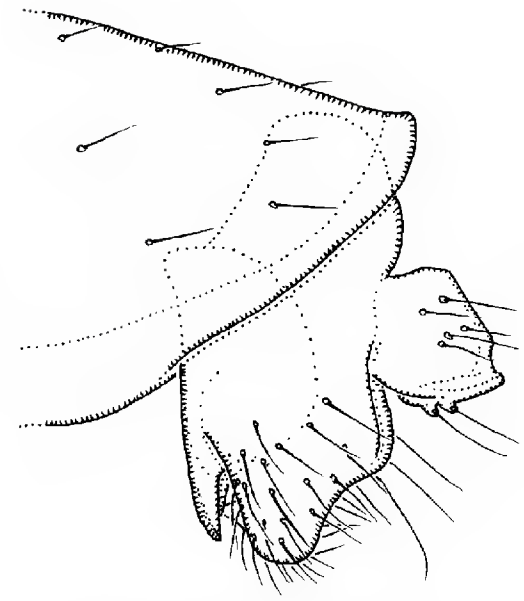
Abbreviations: cerc – cercus; epand – epandrium.



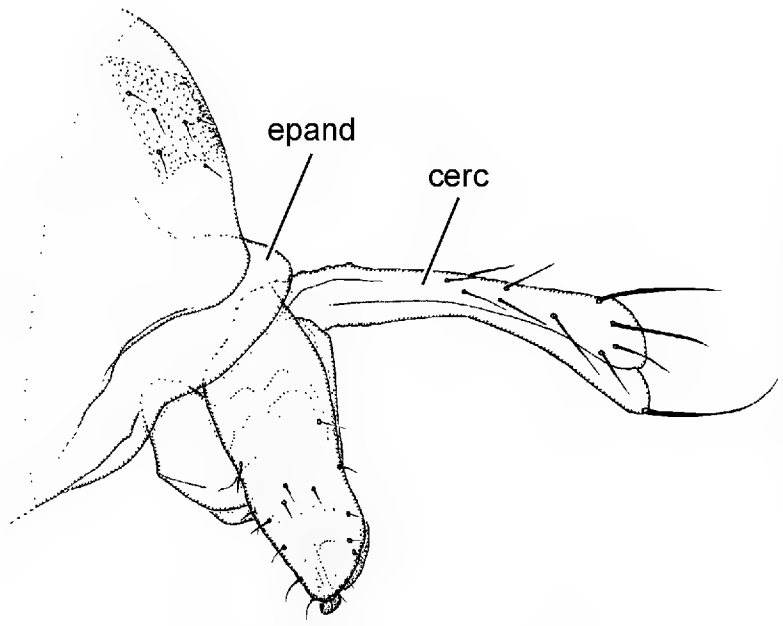
211 *Thaumatoxena* ♂



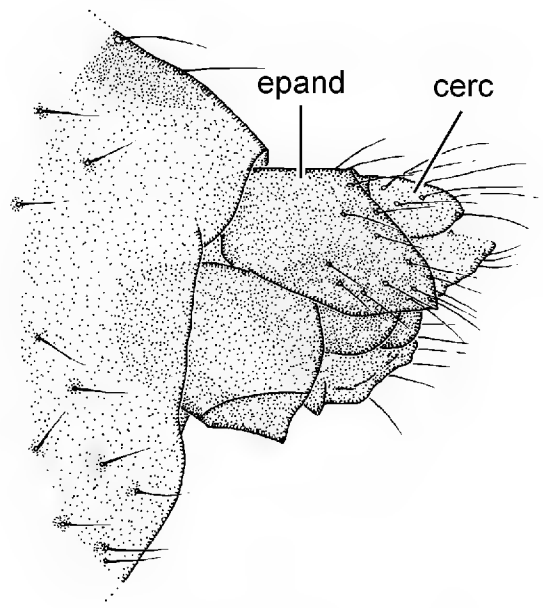
212 *Thaumatoxena* ♂



213 *Thaumatoxena* ♂



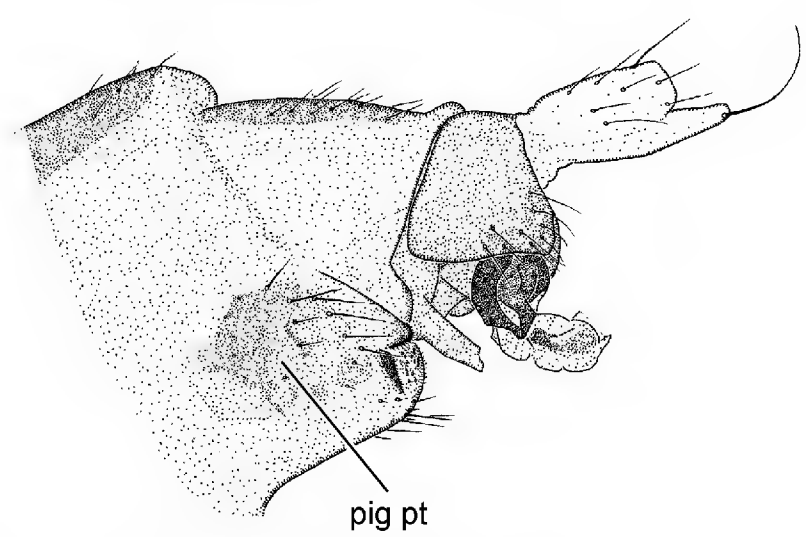
214 *Veranophora* ♂



215 *Woodiphora* ♂

216 *Rhynchomicropteron* ♂

217 *Rhynchomicropteron* ♂



218 *Plastoporides* ♂

Figs 59.211–218. Male terminalia (hypopygia) of Phoridae: (211) *Thaumatoxena andreinii* Silvestri, ventral view; (212) same, dorsal view; (213) same, left lateral view; (214) *Veranophora medleri* (Disney), left lateral view; (215) same, *Woodiphora afrotropica* Disney; (216) *Rhynchomicropteron* sp., right lateral view (non-Afrotropical); (217) same, left lateral view; (218) same, *Plastophorides* sp. Figs 211–213 (Disney & Kistner 1992, figs 39–41), Figs 214, 215 (Disney 2006, figs 112, 121), Figs 216, 217 (Disney 2012*b*, figs 14, 15), Fig. 218 (Disney 1994, fig. 8.71a).

Abbreviations: cerc – cercus; epand – epandrium; pig pt– pigmentation patch.

regions, except Antarctica. Six species occur in the Afrotropics distributed in Central and Southern Africa. Biology and immature stages remain unknown, but elsewhere several species are parasitoids of other insects and some are spider egg predators. Afrotropical species were treated by Beyer (1965), supplemented by Disney (2012*a*) and Schmitz (1932).

***Phlebothrix* Borgmeier** (Phorinae)**.** An endemic genus of two species, *P. cochleariapalpis* (Speiser, 1908), recorded from Madagascar, South Africa and Tanzania and *P. judithmastersae* Mostovski, 2004, described from South Africa. Biology and immature stages remain unknown. The species were treated by Mostovski (2004) and Schmitz (1929: 100) (as *Nossibea*).

[***Phora* Latreille** (Phorinae)**.** A genus of *ca* 80 species, occurring in the Afrotropical, Nearctic, Neotropical, Oriental and Palaearctic Regions. The single enigmatic Afrotropical species, *P. congolensis* (Beyer, 1965), was described from Rwanda, but Mostovski (2016) has questioned the validity of the species].

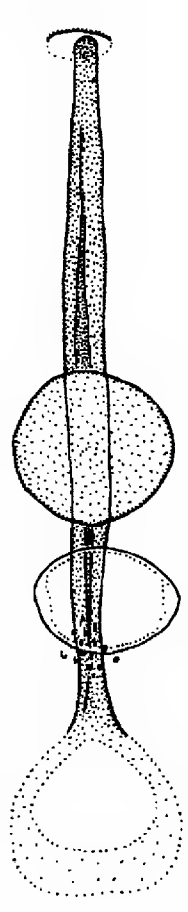
***Plastophorides* Beyer** (Metopininae: Gymnophorini)**.** A genus of four species occurring in the Afrotropical and Oriental Regions. The single Afrotropical species, *P. aculeipes* (Collin, 1912), is recorded from Angola, Democratic Republic of Congo and Seychelles. Biology and immature stages remain unknown. The species was included in an identification key provided by Almond (2002).

***Plethysmochaeta* Schmitz** (Phorinae)**.** A genus of six species, occurring in the Afrotropical, Oriental and Palaearctic Regions. Five species are widely distributed in the continental Afrotropics. Females of *P. trinervis* were caught at a putrefying mollusc (*Unio* sp.) (Schmitz 1916) and a female of *P. couvreuri* Schmitz, 1953, at an Impala carcass. The immature stages remain unknown. An identification key treating seven species, including the five Afrotropical species, was provided by Disney (1995*a*) and an additional Afrotropical species was added by Hibbs & Brown (1998).

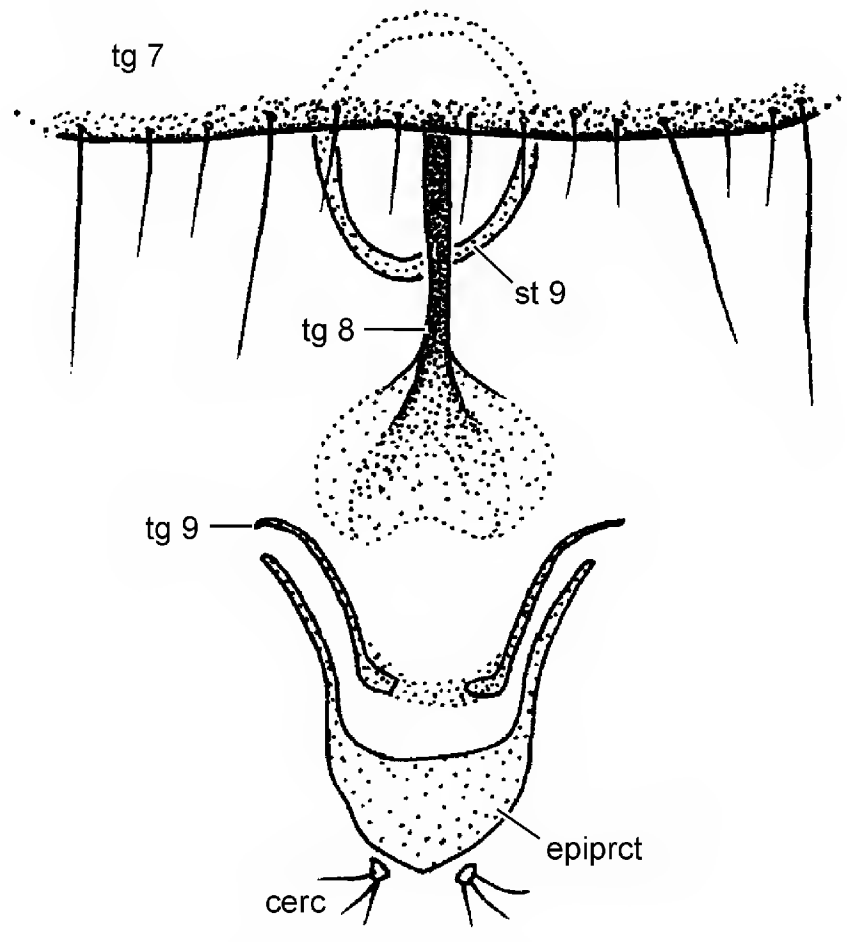
***Psyllomyia* Loew** (Phorinae: Aenigmatiini)**.** A genus of 12 species occurring in the Afrotropical and Oriental Regions. Seven Afrotropical species are distributed in Kenya and South Africa. Adults have been recorded from the colonies of driver ants (*Dorylus*), but the immature stages remain unknown. An identification key to the seven Afrotropical species was provided by Disney & Kistner (1998).

***Ptochomyia* Silvestri** (Phorinae: Termitoxeniini)**.** An endemic genus of three species, *P. afra*, recorded from Cameroon, Guinea and Nigeria, *P. alticola* Schmitz, 1958, described from Angola and *P. cummingae*, described from Zimbabwe. Adults are recorded with colonies of the termites *Ancistrotermes cavithorax*, *A. crucifer* and *A. latinotus*, but the immature stages otherwise remain unknown. The three species were treated by Disney & Kistner (1995).

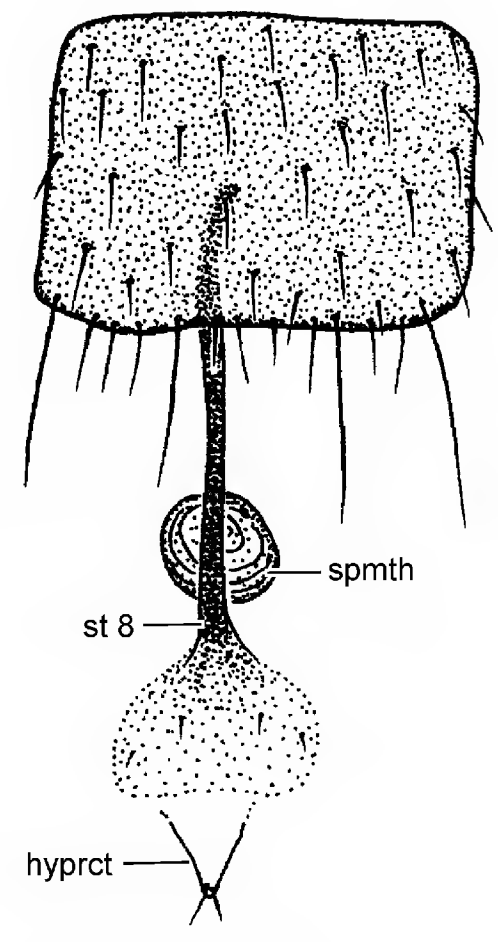
***Puliciphora* Dahl** (Metopininae: Metopinini)**.** A large genus of *ca* 100 species occurring in all zoogeographical regions, except Antarctica. A dozen species occur in the Afrotropical Region, widely distributed in the continental Afrotropics, Cabo



219 *Chonocephalus* ♀



220 *Chonocephalus* ♀



221 *Chonocephalus* ♀

Figs 59.219–221. Female terminalia of Phoridae: (219) internal terminalia of *Chonocephalus dominicanus* Borgmeier, dorsal view; (220) same, *Chonocephalus* sp.; (221) same, ventral view. Fig. 219 (Disney 2009*b*, fig. 22), Figs 220, 221 (Disney 1994, figs 8.8a, 8.8b).

Abbreviations: cerc – cercus; epiprct – epiproct; hyprct – hypoproct; spmth – spermatheca; st – sternite; tg – tergite.

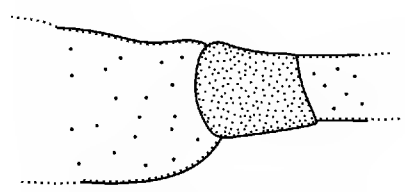
Verde and Madagascar, the Southern Arabian Peninsula and Seychelles. Species recognition is based on flightless females in the first instance and most males can only be named by association with females. Several species have been reared from dead insects, other arthropods and snails. Others breed in ripe fruits, such as those of Pandaceae. Adults of two species have been recorded from the raiding columns and middens of *Dorylus* ants and at termite (*Odontotermnes*) mounds. A revised identification key to the females of Afrotropical species provided by Disney & Kistner (1998), should be supplemented with Disney & Darlington (1998), Disney (2002, 2008*b*: 631, 2009*c*) and Disney & Kistner (1989) for the species previously assigned to *Mesopathusa* Schmitz. Species previously assigned to *Coridophora* Schmitz, known only from females, were treated by Borgmeier (1959) (as *Edaphomyia*) and Disney (1982*a*, 2005*d*). Furthermore, *P. nigriventris* (Borgmeier, 1959) was synonymised with *P. convexa* (Borgmeier, 1960) (Disney 1994: 272). Arabian species were treated by Disney (2006: 503) and those of Seychelles by Disney (2009*b*: 219).

***Razorfemora* Disney** (Metopininae: Gymnophorini)**.** A genus of two species occurring in the Afrotropical and Palaearctic Regions. One species, *R. nussbaumi* Disney, 2006, was described from Yemen in the Southern Arabian Peninsula. The species in Israel and Spain is a parasitoid of the seed harvester ant *Messor barbarus* (L.) (Delgado *et al*. 2020), but biology and immature stages otherwise remain unknown. Both species were treated by Disney (2006: 507).

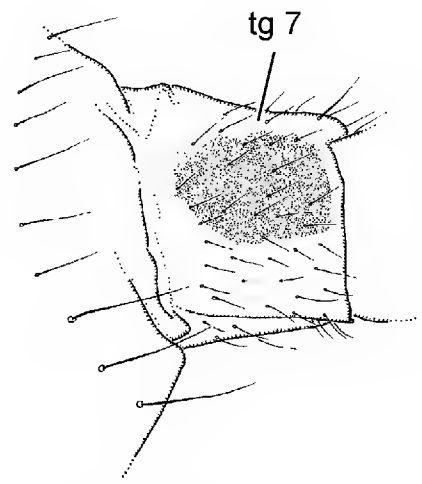
***Ritchiephora* Disney** (Metopininae: Gymnophorini)**.** An endemic monotypic genus with the single species, *R. diplopodae* Disney & Ritchie, 1997, described from Kenya. The species was reared from an immature male millipede of the family Odontopygidae. The species was treated by Disney & Ritchie (1997).

***Rhynchomicropteron* Annandale** (Metopininae: Metopinini)**.** A genus of *ca* 12 species, occurring in the Afrotropical, Oriental and Palaearctic Regions. Mostovski (2016) noted that *R. kuslitzkyi* Lengyel, 2011, described from Israel, may occur in West Africa. Biology and immature stages remain unknown. An identification key to males was provided by Disney (2012*b*).

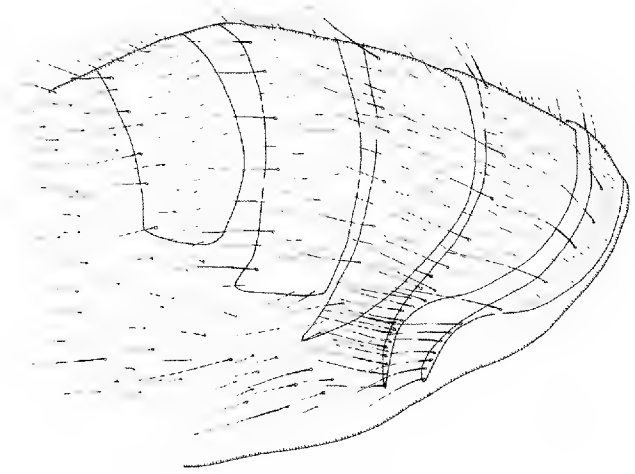
***Stichillus* Enderlein** (Phorinae: Hypocerini)**.** A genus of *ca* 30 species, occurring in all zoogeographical regions, except



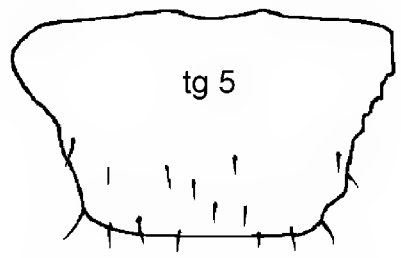
222 *Conicera* ♀

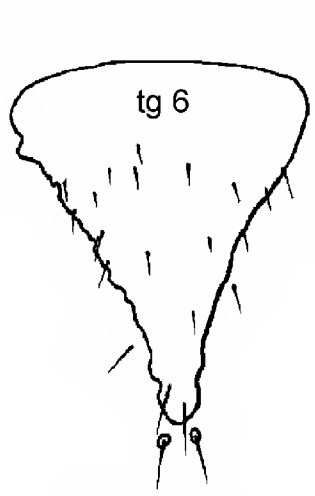


224 *Dohrniphora* ♀

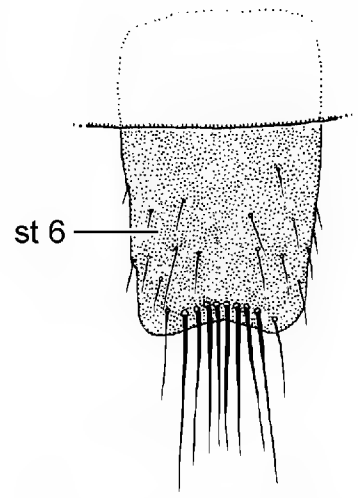


225 *Dundophora* ♀

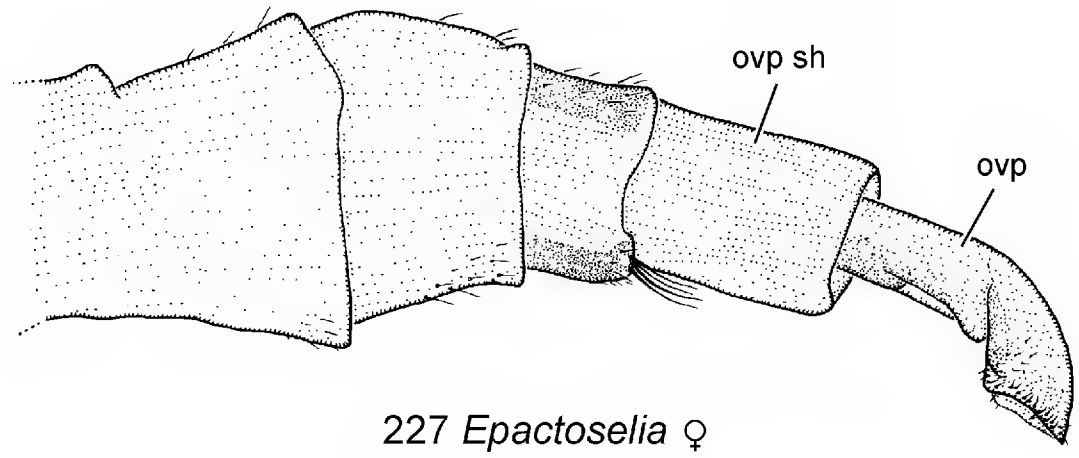




223 *Conicera* ♀



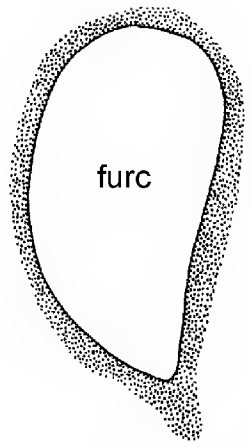
226 *Epactoselia* ♀



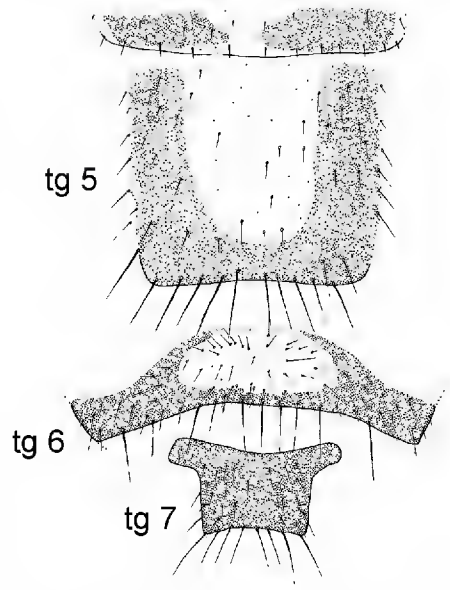
227 *Epactoselia* ♀

Figs 59.222–227. Female abdomens and terminalia of Phoridae: (222) vaginal sclerite (furca) of *Conicera tibialis* Schmitz, lateral view; (223) abdominal tergites 5 and 6 of *C. tibialis*, dorsal view; (224) abdominal segment 6 and 7 of *Dohrniphora cornuta* (Bigot *in* de la Sagra), lateral view; (225) abdominal tergites 1–5 of *Dundophora fimbriiterga* (Schmitz), lateral view; (226) abdominal sternite 6 of *Epactoselia provallaris* Disney, ventral view; (227) same, terminal segments of abdomen, lateral view. Figs 222, 223 (Disney *et al*. 2010, figs 6B, 6C), Figs 224, 225 (Disney 1994, figs 8.40c, 8.41a), Figs 226, 227 (Disney & Kistner 1998, figs 10, 11).

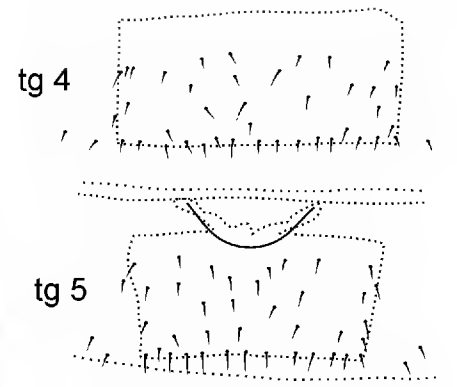
Abbreviations: ovp – ovipositor; ovp sh – ovipositor sheath; st – sternite; tg – tergite.



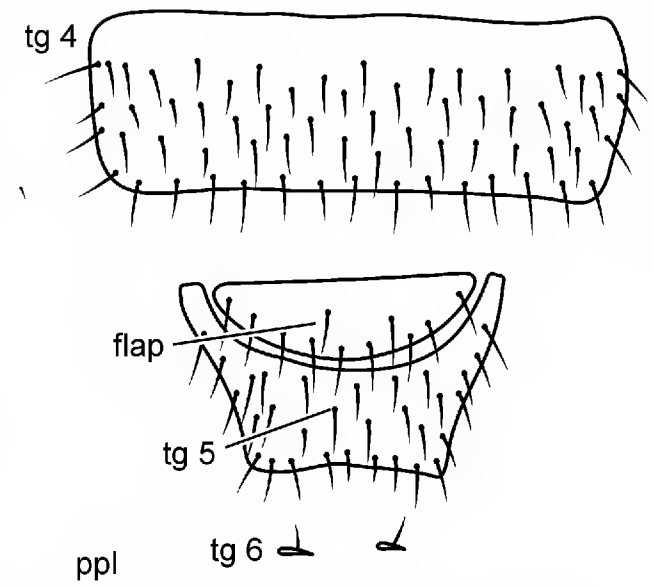
228 *Megaselia* ♀



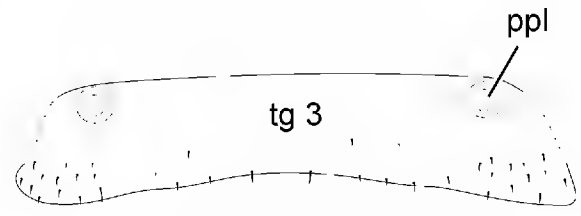
229 *Megaselia* ♀



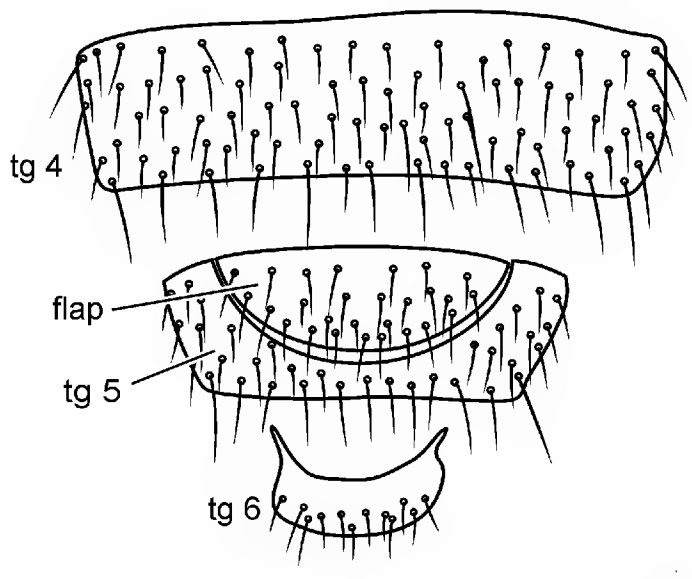
230 *Metopina* ♀



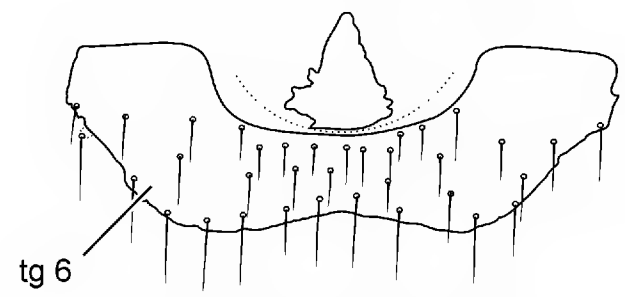
231 *Puliciphora* ♀



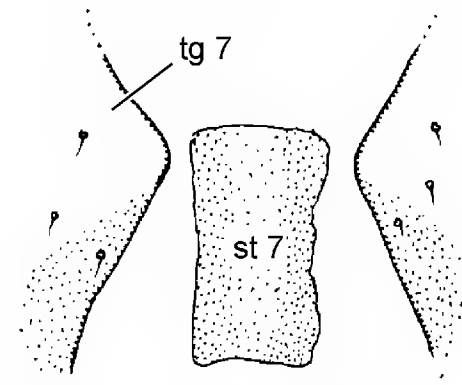
233 *Phalacrotophora* ♀



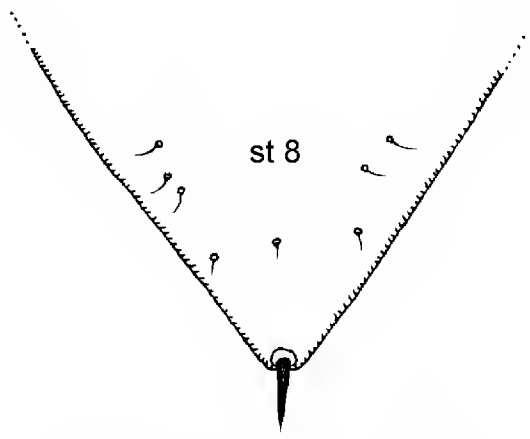
232 *Puliciphora* ♀



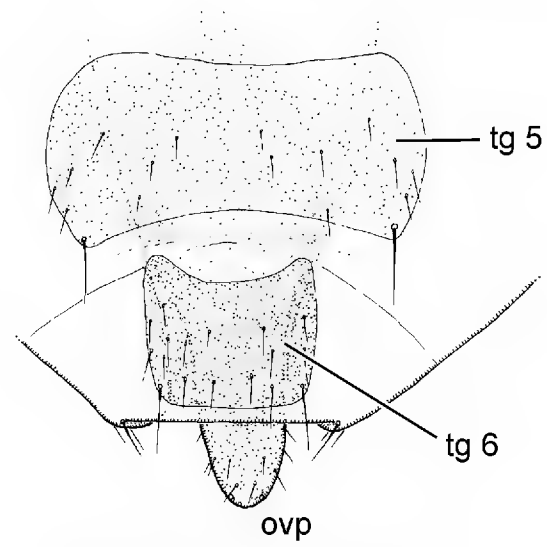
234 *Woodiphora* ♀



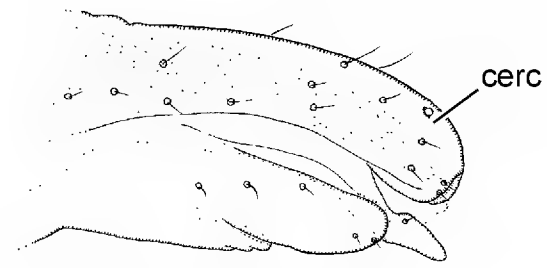
235 *Veranophora* ♀



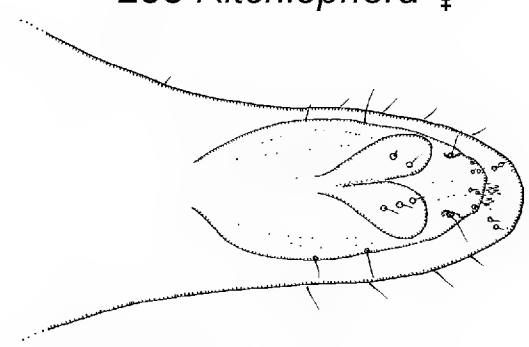
236 *Veranophora* ♀



237 *Ritchiephora* ♀



238 *Ritchiephora* ♀



239 *Ritchiephora* ♀

Figs 59.228–239. Female abdomens and terminalia of Phoridae: (228) furca (internalised sternite 9) of *Megaselia scalaris* Loew, lateral view; (229) same, abdominal tergites 4–7, dorsal view; (230) abdominal tergites 4 and 5 of *Metopina ciceri* Disney, dorsal view; (231) abdominal tergites 4–6 of *Puliciphora pulex* Dahl (tergite 6 represented by anterior apodemes only), dorsal view; (232) abdominal tergites 4–6 of *Pu. borinquenensis* Wheeler, dorsal view; (233) abdominal tergite 3 of *Phalacrotophora* sp., dorsal view; (234) abdominal tergite 6 of *Woodiphora afrotropica* Disney, dorsal view; (235) sternite 7 and lateral edges of tergite 7 of *Veranophora medleri* (Disney), ventral view; (236) tip of sternite 8 of *V. medleri*, ventral view; (237) tergites 5 and 6 and tip of ovipositor sheath of *Ritchiephora diplopodae* Disney, dorsal view; (238) same, ovipositor sheath and tip of ovipositor, left lateral view; (239) same, tip of abdomen, ventral view. Fig. 228 (Disney 2008*b*, fig. 94), Fig. 229 (Disney 1991*c*, 41), Fig. 230 (Disney 1988, fig. 5), Figs 231, 234–236 (Disney 2006, figs 84, 123, 114, 115, respectively), Figs 232, 233 (Disney 1994, figs 6.14b, 8.70a), Figs 237–239 (Disney & Ritchie 1997, figs 4–6).

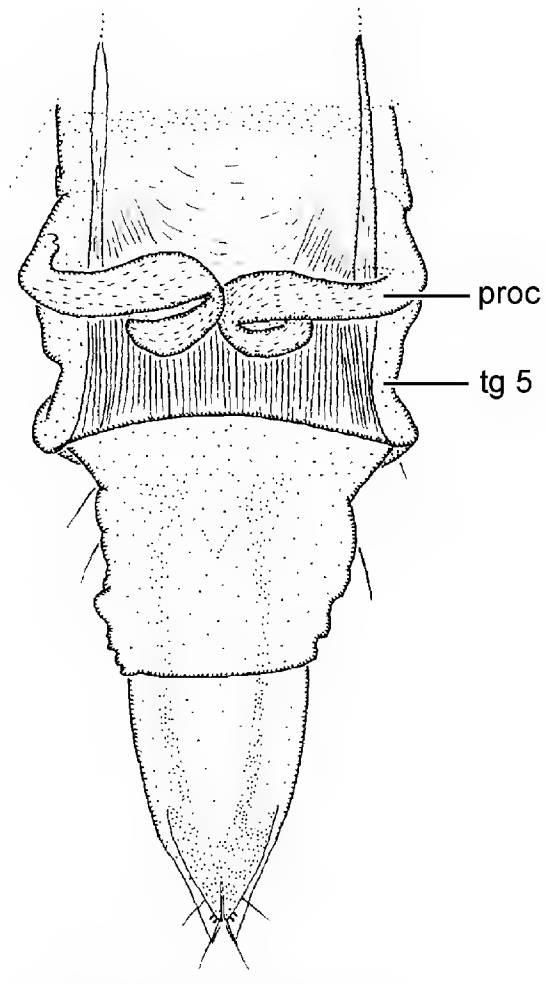
Abbreviations: cerc – cercus; furc – furca; ovp – ovipositor; ppl – papilla; st – sternite; tg – tergite.

Antarctica. The single Afrotropical species, *S. necopinatus* Beyer, 1960, was described from South Africa. Biology and immature stages remain unknown. The species was treated by Mostovski (2004), who re-described the species.

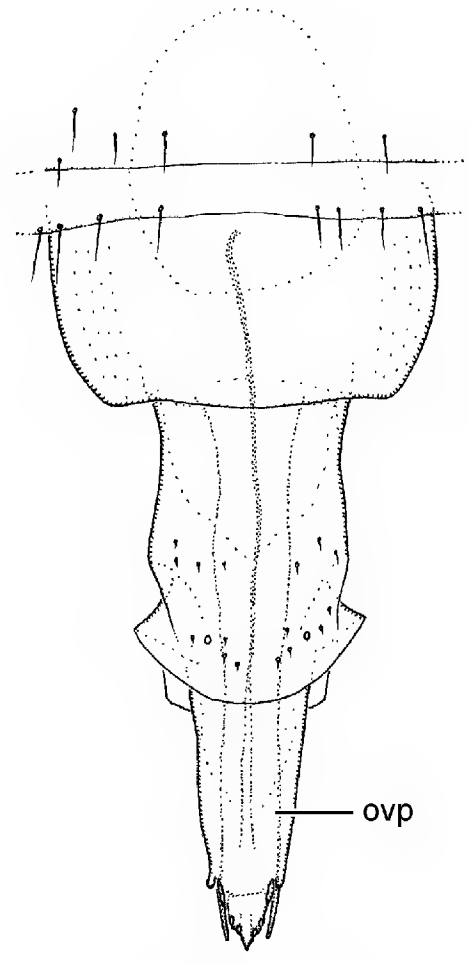
***Synaptophora* Brown** (Phorinae)**.** An endemic monotypic genus with the single species, *S. critica* Brown, 1992, known only from females described from Uganda. Biology and immature stages remain unknown. The species was treated by Brown (1992).

***Syntermitoxenia* Schmitz** (Phorinae: Termitoxeniini)**.** An endemic genus of six species, distributed in East, Southern and West Africa. Adults have been recorded in colonies of termites, *i.e.*, *S. extra* and *S. jaegerskioeldi* with the termites *Odontotermes interveniens* and *Od. latericius* and the latter species also with the termite *Od. lacustris*, but immature stages remain unknown. The six species were treated by Disney & Kistner (1995).

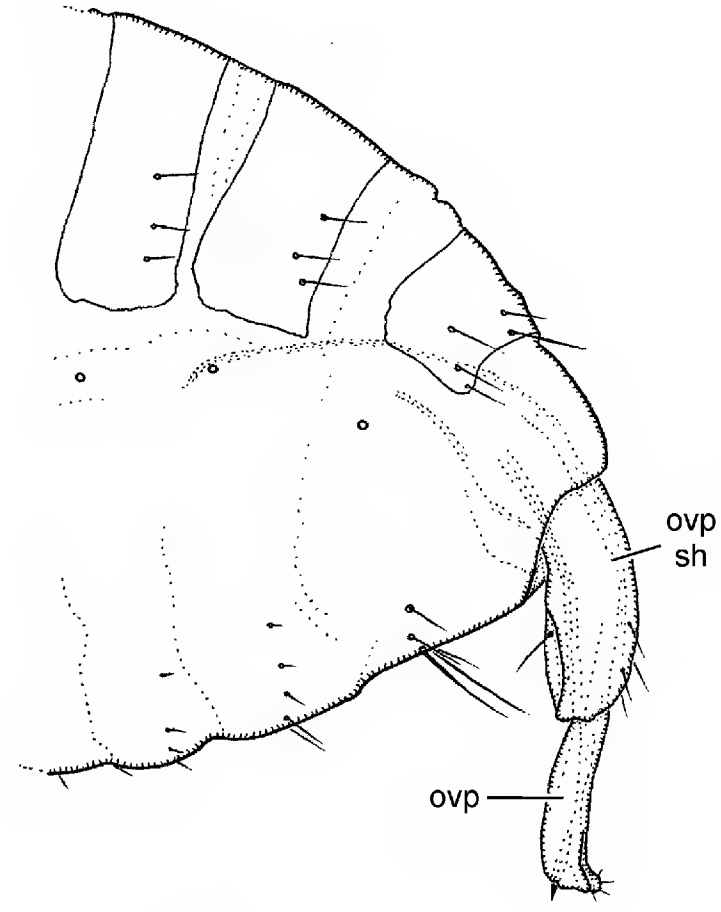
***Termitomyia* Wasmann** (Phorinae: Termitoxeniini)**.** An endemic monotypic genus with the single species, *T. mirabilis*,



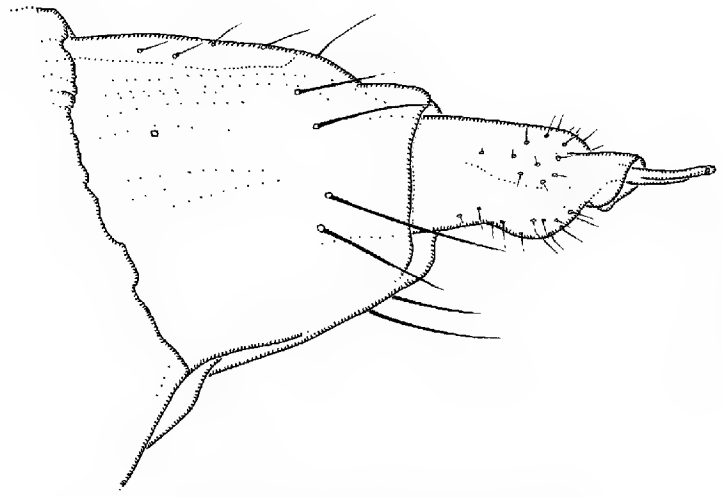
240 *Menozziola* ♀



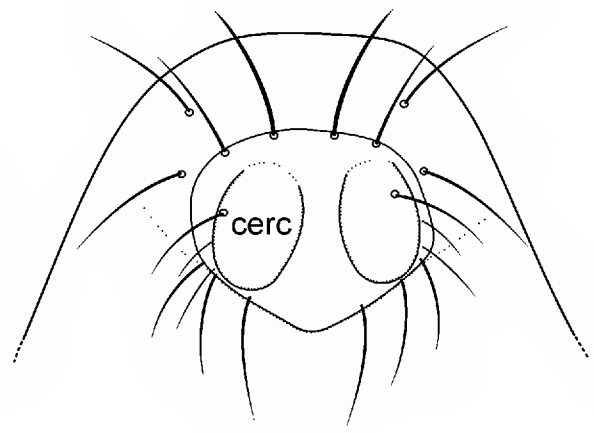
241 *Microselia* ♀



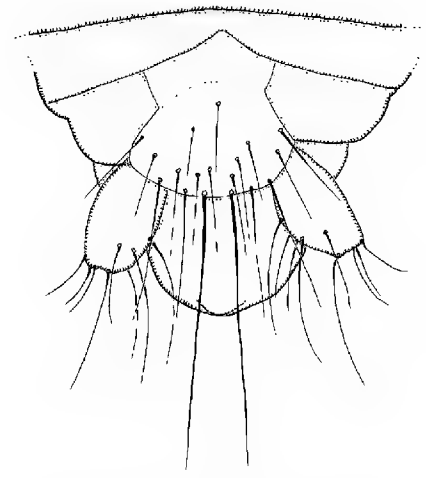
242 *Miclepta* ♀



243 *Plastophorides* ♀



244 *Paratermitoxenia* ♀



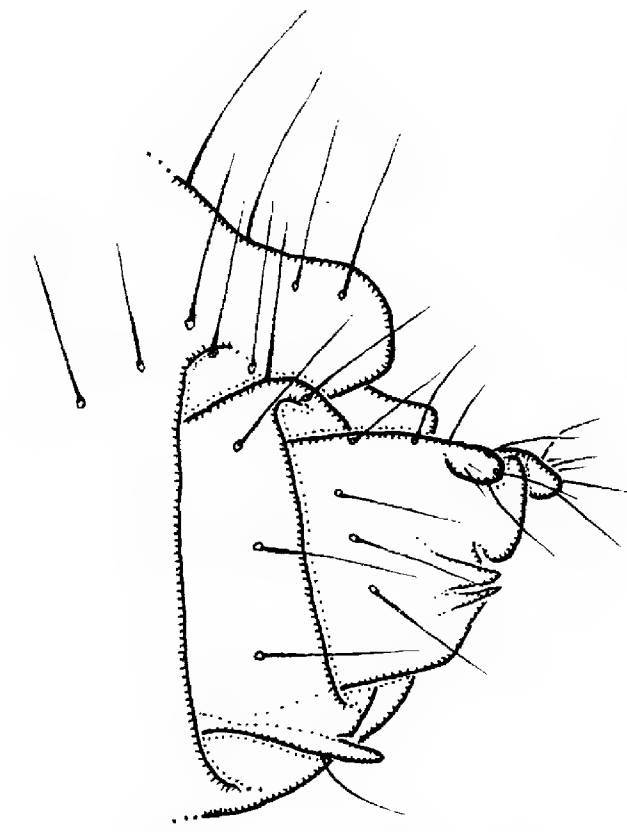
245 *Phlebothrix* ♀

Figs 59.240–245. Female abdominal segments and terminalia of Phoridae: (240) terminal abdominal segments of *Menozziola schmitzi* (Menozzi), ventral view (non-Afrotropical); (241) same, *Microselia yemenensis* Disney, dorsal view; (242) same, *Miclepta arrujumensis* Disney, left lateral view; (243) same, *Plastophorides aculeipes* (Collin); (244) tip of abdomen of *Paratermitoxenia coatoni* Beyer, posterior view; (245) same, *Phlebothrix cochlearipalpis* (Speiser), dorsal view. Fig. 240 (Disney 1994, fig. 2.6), Figs 241, 242 (Disney 2006, figs 70, 61, respectively), Fig. 243 (Disney 1991*a*, fig. 31), Fig. 244 (Disney & Kistner 1995, fig. 23), Fig. 245 (Disney 2009*b*, fig. 153).

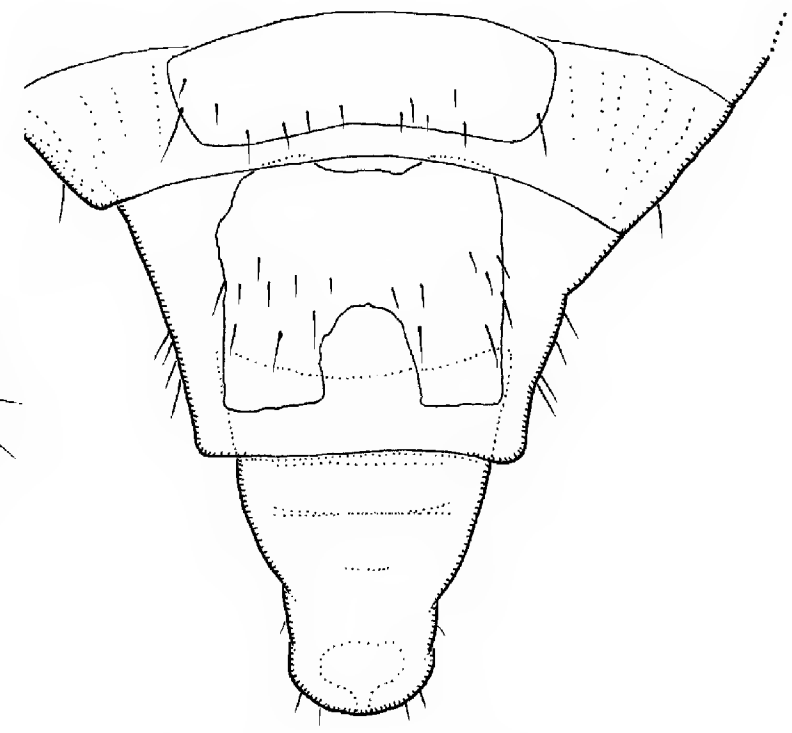
Abbreviations: cerc – cercus; ovp – ovipositor; ovp sh – ovipositor sheath; proc – process; tg – tergite.

known only from females described from South Africa. Adults have been recorded in colonies of the termites *Odontotermes capensi* and *Od. vulgaris*, but the immature stages remain unknown. The species was treated by Disney & Kistner (1995).

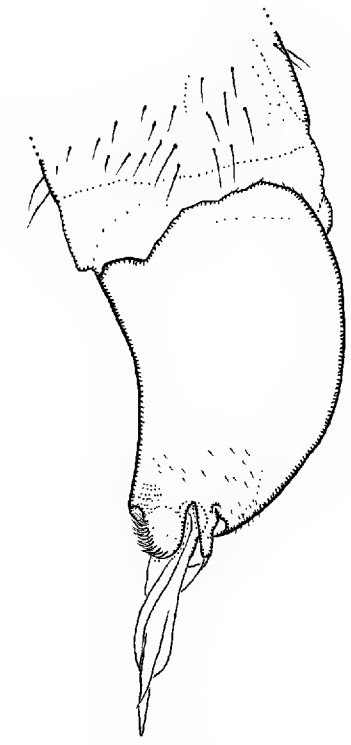
Termitophilomyia **Schmitz** (Phorinae: Termitoxeniini)**.** An endemic genus of seven species, widely distributed in the continental Afrotropics. Adults have been recorded in colonies of the termite genus *Odontotermes*: *T. braunsi* with *Od. latericius* and *Od. transvaalensis*; *T. gracilis* with *Od. badius*, *Od. culturarum*, *Od. montanus* and *Od. nolaensis*; *T. leleupi* with *Od. okahandjae* and *Od. fulleri*; *T. papillacollaris* with *Od. transvaalensis*; *T. uvirana* with *Od. fulleri*, *Od. nolaensis* and *Od. planiceps*; *T. zimbraunsi* with *Od. latericius* and *Od. transvaalensis*; but the immature stages remain unknown. The seven species were treated by Disney & Kistner (1995).



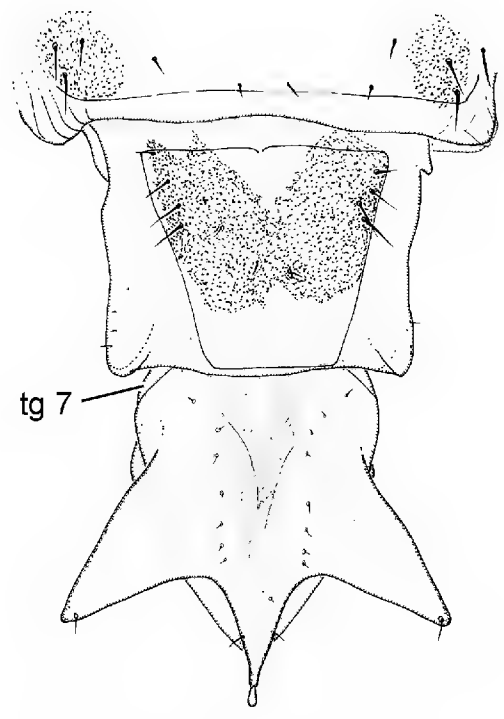
246 *Termitomyia* ♀



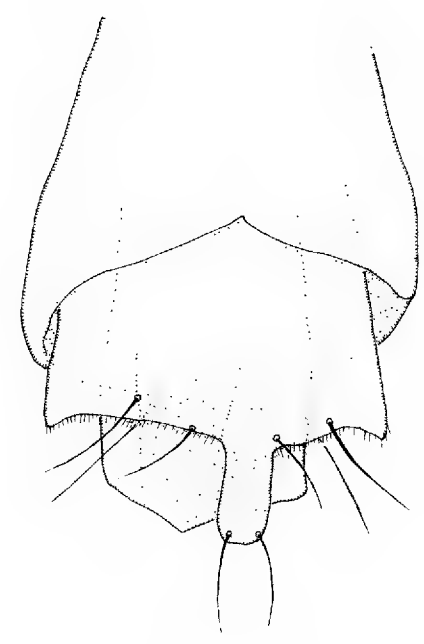
247 *Razorfemora* ♀



248 *Razorfemora* ♀



249 *Veranophora* ♀



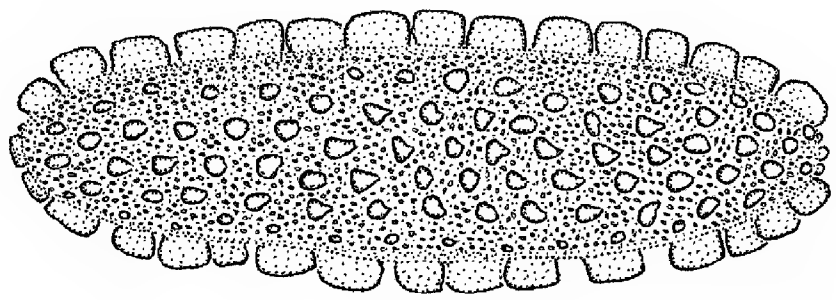
250 *Termitoscrofa* ♀

Figs 59.246–250. Female abdomens and terminalia of Phoridae: (246) tip of abdomen of *Termitomyia mirabilis* (Wasmann), left lateral view; (247) terminal abdominal segments of *Razorfemora nussbaumi* Disney, dorsal view; (248) ovipositor tip and sheath of *R. nussbaumi* Disney, left lateral view; (249) terminal abdominal segments of *Veranophora medleri* (Disney), dorsal view; (250) abdominal segment 7 of *Termitoscrofa brevis* Delachambre, ventral view. Fig. 246 (Disney & Kistner 1995, fig. 71), Figs 247, 248 (Disney 2006, figs 92, 93), Fig. 249 (Disney 1994, fig. 2.5), Fig. 250 (Disney & Kistner 1995, fig. 119).

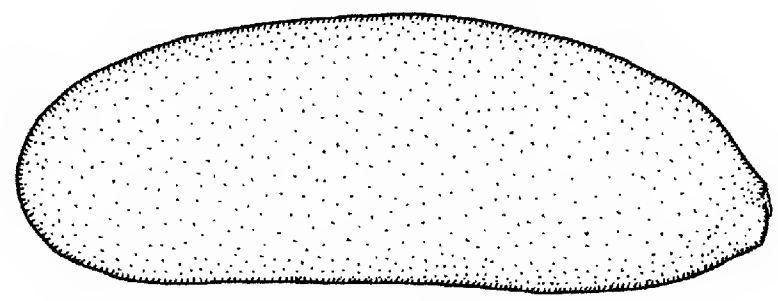
Abbreviation: tg – tergite.

***Termitophorina* Borgmeier** (Metopininae)**.** An endemic monotypic genus with the single species, *T. africana* Borgmeier, 1976, known only from females described from Democratic Republic of Congo. It was recorded with an unidentified termite. Its immature stages remain unknown. The species was treated by Borgmeier (1967).

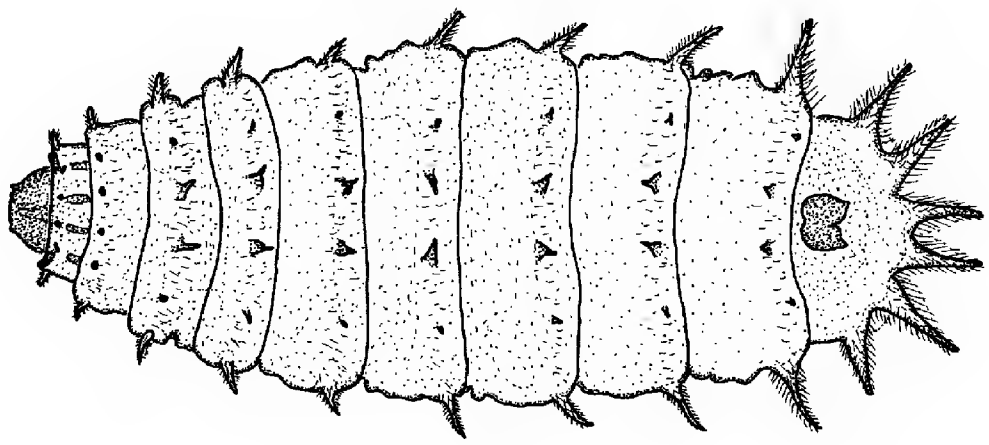
***Termitosagma* Reichensperger** (Phorinae: Termitoxeniini)**.** An endemic monotypic genus with the single species, *T. henningsi*, recorded from Angola, Democratic Republic of Congo, Kenya and Tanzania. Adults are recorded from colonies of the termites *Odontotermes badius*, *Od. culturarum* and *Od. partruus*, but the immature stages remain unknown. Females



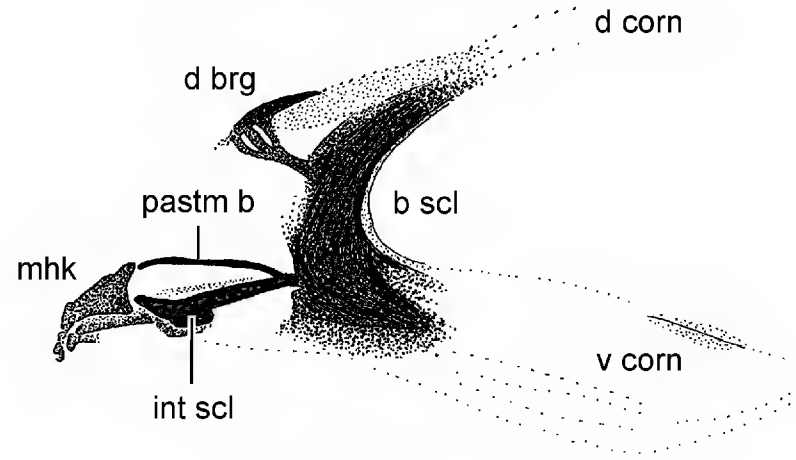
251 *Megaselia*



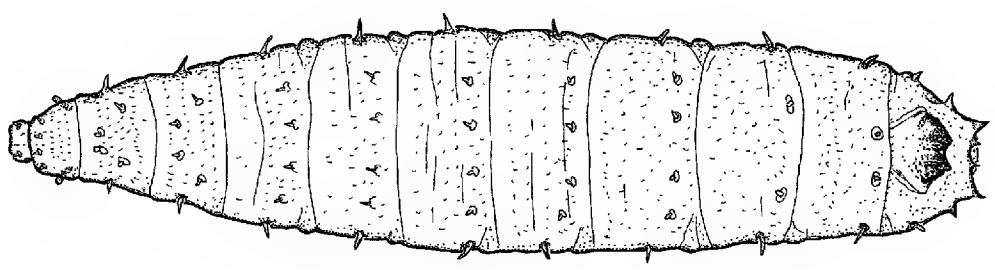
252 *Puliciphora*



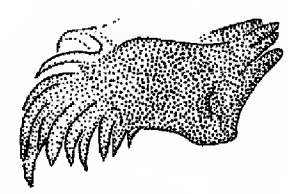
253 *Dohrniphora*



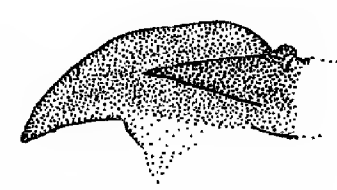
255 *Megaselia*



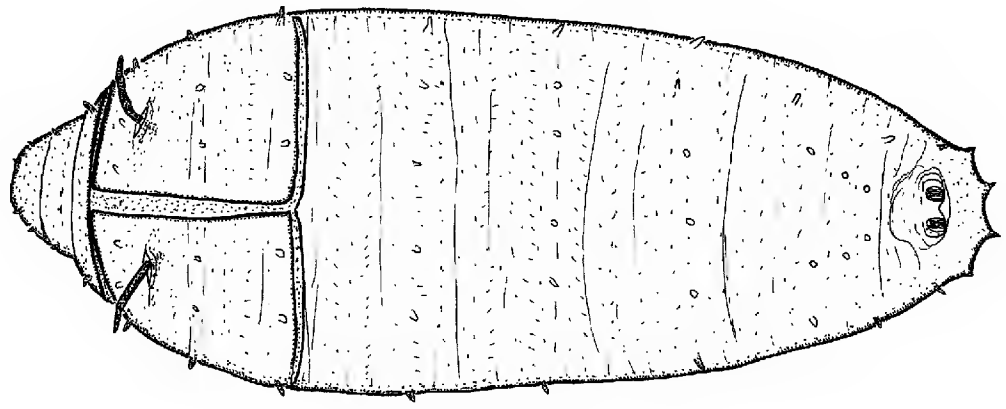
254 *Megaselia*



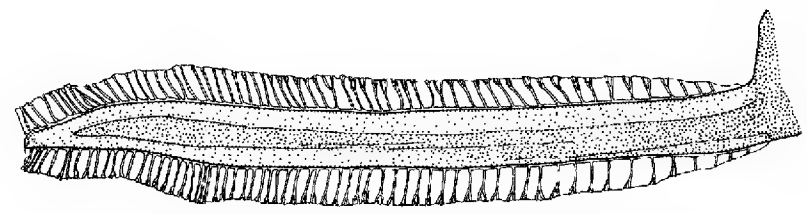
256 *Megaselia*



257 *Megaselia*



258 *Megaselia*



259 *Dohrniphora*

Figs 59.251–259. Immature stages of Phoridae: (251) egg of *Megaselia scalaris* Loew, dorsal view of plastron (most eggs of *Megaselia* lack a plastron); (252) same, *Puliciphora borinquenensis* Wheeler; (253) habitus of third-instar larva of *Dohrniphora cornuta* (Bigot *in* de la Sagra), dorsal view; (254) same, *M. rufipes* (Meigen); (255) cephaloskeleton of *M. scalaris*, lateral view; (256) mouthhooks of *M. scalaris*, lateral view; (257) same, median tooth, lateral view; (258) habitus of puparium of *M. rufipes*, dorsal view; (259) puparial respiratory horn of *D. cornuta*, dorsal view. Figs 251, 257 (Disney 2008*b*, figs 99, 98, respectively), Fig. 252 (Disney 2009*b*, fig. 168), Figs 253–256, 258, 259 (Disney 1994, figs 3.1a, 3.1b, 3.4d, 3.4c, 4.1, 4.5, respectively),

Abbreviations: b scl – basal sclerite; d brg – dorsal bridge; d corn – dorsal cornu; int scl – intermediate sclerite; mhk – mouthhook; pastm b – parastomal bar; v corn – ventral cornu.

steal food from the nymphs and younger larvae of their termite hosts. The species was treated by Disney & Kistner (1995) and the male by Disney & Darlington (2000*a*).

Termitoscrofa **Schmitz** (Phorinae: Termitoxeniini)**.** An endemic genus of three Afrotropical species, *T. brevis*, described from Côte d'Ivoire, *T. mellea* (Borgmeier, 1963), described from Ethiopia and *T. pinguissima*, recorded from Kenya and Tanzania. All three species are only known from females from the colonies of the termites *Megaprotermes giffardii* and *T. pinguissima* with *Odontotermes badius* and *Od. montanus*. The three species were treated by Disney & Kistner (1995).

Termitostroma **Reichensperger** (Phorinae: Termitoxeniini)**.** An endemic monotypic genus with the single species, *T. schmitzi*, known only from females and recorded from Democratic Republic of Congo, Malawi, South Africa, Tanzania, Zambia and Zimbabwe. Adults are associated in colonies of the termites *Odontotermes badius*, *Od. patruus* and *Od. culturarum*, but immature stages remain unknown. The species was treated by Disney & Kistner (1995).

Termitoxenia **Wasmann** (Phorinae: Termitoxeniini)**.** An endemic genus of four species, *T. havilandi*, recorded from Malawi, Mozambique and South Africa, *T. kistnerorum*, described from Angola, *T. oligoseta* described from Zimbabwe and *T. parvicaliculorum* Disney, 1996, described from Botswana and Zimbabwe. All four are only known from females from colonies of the termite genus *Odontotermes*. *Termitoxenia havilandi* is associated with the termite *Od. latericius*; *T. kistnerorum* with *Od. interveniens*, *Od. lacustris* and *Od. latericius*; and *T. oligoseta* with *Od. lacustris*, but immature stages remain unknown. Species were treated by Disney & Kistner (1995), supplemented by Disney (1996).

Thaumatoxena **Breddin & Börner** (Phorinae: Thaumatoxenini)**.** An endemic genus of nine species, distributed in East, Southern and West Africa. Females were recorded from the fungus gardens of termites of the genus *Macrotermes*, but immature stages remain unknown. An identification key to species was provided by Disney & Kistner (1992), supplemented by Disney (2006: 508) and Disney & Darlington (2000*b*).

Veranophora **Disney** (Metopininae)**.** An endemic monotypic genus with the single species, *V. medleri* (Disney, 1981) recorded from Nigeria, Senegal, Yemen and Zimbabwe. Biology and immature stages remain unknown. The species was transferred from the genus *Auxanommatidia* Borgmeier and was treated by Disney (1981*a*, 2003*c*).

Wandolleckia **Cook** (Metopininae: Metopinini)**.** An endemic monotypic genus with the single species, *W. achatinae*, recorded from Cameroon, Democratic Republic of Congo, Kenya, Liberia, Sierra Leone and Tanzania. Adults and larvae feed on the dung of *Achatina* snails (Baer 1953) (see Chapter 4, Fig. 4.49). The immature stages were described by Baer (1953) (who included figures of the male anal tube as the "penis" in error). The female was also figured by Schmitz (1916).

Woodiphora **Schmitz** (Metopininae: Gymnophorini)**.** A genus of *ca* 50 species occurring in all zoogeographical regions, except Antarctica. Six species occur in the Afrotropics, distributed in Cabo Verde, Cameroon, Côte d'Ivoire, Seychelles, Yemen and Zambia. Two Oriental species have been caught at ant and termite colonies. The biology and immature stages of Afrotropical species remain unknown. An identification key to Afrotropical species was provided by Disney (1985*b*), supplemented by Disney (1991*c*, 2004*b*, 2005*c*, *e*, 2006: 511).

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SYRPHIDAE 60

(Flower Flies or Hoverflies)

Axel Ssymank, Kurt Jordaens, Marc De Meyer, Menno Reemer and Graham E. Rotheray

Fig. 60.1. Male of *Afromicrodon* sp. (Madagascar) (photograph © S.A. Marshall).

Diagnosis

Small- to large-sized flies (body length: 4–25 mm), with petiolate or slender to wide and robust body; colouration often brown to black, with yellow or red abdominal markings (Figs 3, 4, 6, 9), others entirely black (Figs 2, 8, 64) or metallic green to blue (Figs 60, 62, 82); mimetic shape and colour patterns frequent, e.g., in *Afrosyrphus* Curran (Fig. 43) (proposed models: Apidae: Apinae: *Apis* L.), *Ceriana* Rafinesque (Fig. 54) (proposed models: Eumenidae: e.g., *Rhynchium marginellum* (F.) for *C. ponti* Thompson, 2013), *Monoceromyia* Shannon (Fig. 80) and *Sphiximorpha* Rondani (Fig. 96) (proposed models for smaller species of both genera: Vespidae: Polistinae: *Polistes* Latreille, *Ropalidia* Guérin-Méneville and *Belonogaster* de Saussure; for larger species: Eumenidae: *Eumenes* Latreille and *Delta* de Saussure).

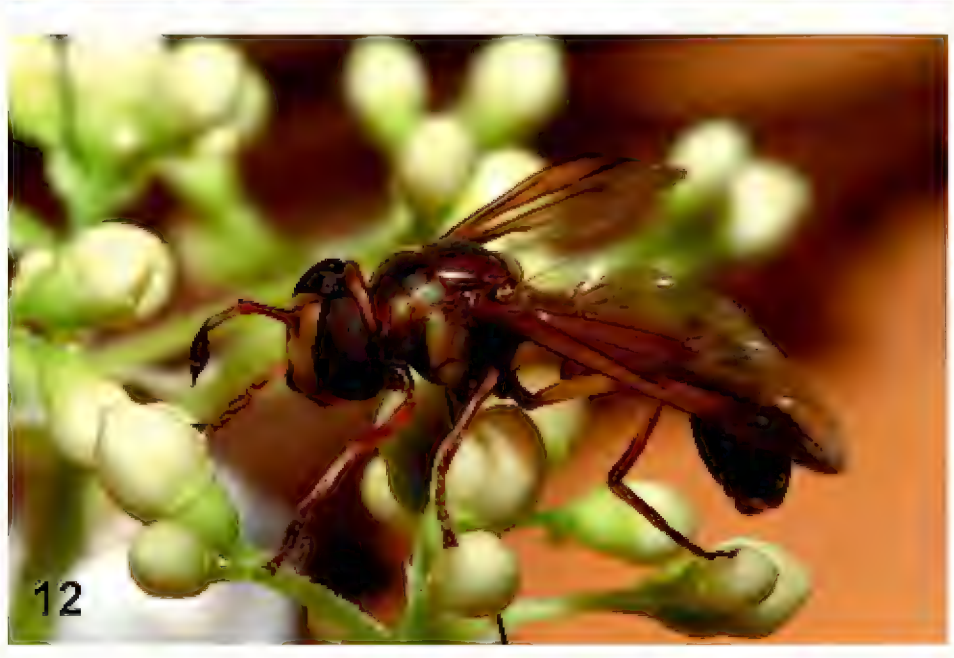
Head with eye bare or pilose; eyes invariably dichoptic in females (Figs 17, 19), usually holoptic in males (Figs 15, 16), except in Afrotropical Microdontinae and some (sub)genera of Eristalinae (*Anasimyia* Shiner, *Chasmomma* Bezzi (Fig. 14), *Rhingia* (*Eorhingia* Hull), *Graptomyza* Wiedemann and *Simoides* Loew (Fig. 18)); 3 ocelli present; antenna short (Figs 23, 32–38) to elongate, pendulous (Figs 24, 28), or forwardly directed ("proerect") (Figs 21, 22, 43), with 3 distinct antennal segments: scape, pedicel and postpedicel, plus apical thickened arista (Fig. 21), or dorsal to sublateral arista (Figs 36, 38, 40); antennae usually inserted directly between face and frons, but in *Monoceromyia* (Figs 21, 80) inserted on long frontal projection; arista bare (Fig. 40), with short micro-pubescence (Fig. 39) or uni- or bi-directional plumose to pectinate (Figs 24, 25); head without setae; facial profile variable, usually with callus (Figs 31, 32, 36), but in some genera face flat (Figs 20, 24–28), or in *Anasimyia* (Fig. 47), some *Graptomyza* (Fig. 67), many *Asarkina* Macquart (Fig. 50) and *Rhingia* Scopoli (Fig. 91), with short to long, proerect "snout".

Thorax (Fig. 112), with postpronotum clearly exposed (Figs 55, 76) or (partly) hidden by closely appressed head (Figs 42, 50); postpronotum setulose (Fig. 103) or bare (Fig. 104);

thoracic setae only present in *Graptomyza* and *Ornidia* Le Peletier & Serville; plumula (*i*.e., fringed posteroventral extension of subalar sclerite), short to long, rarely absent, in the Microdontinae, but short or absent in *Spheginobaccha* de Meijere; setulae on thorax variable in form and distribution on postpronotum, scutum, scutellum and pleura. Scutellum with (Fig. 111), or without, subscutellar fringe; metasternum complete (Fig. 118) or greatly reduced (Fig. 119); postmetacoxal bridge present (Fig. 113) or absent. Wing with large basal cells *br*, *bm* and *cua*; cell r_{4+5} closed (first branch of vein *M* joining unbranched vein R_{4+5} and crossvein *r–m*) (Fig. 120); spurious vein (longitudinal vein-like thickening in membrane between veins *R* and *M*) usually present (Figs 128–131), but weakly developed in *Graptomyza* (Fig. 144), *Ornidia* (Fig. 159),

Figs 60.2–7. Photographs of living Afrotropical Syrphidae: (2) *Allobaccha* sp. (Tanzania); (3) *Allograpta* sp. (South Africa); (4) *Asarkina* (*Asarkina*) sp. (Kenya); (5) *Betasyrphus intersectus* (Wiedemann) (South Africa); (6) *Chrysotoxum continum* Bezzi (Kenya); (7) *Eristalinus* (*Eristalinus*) *vicarians* Bezzi (Cameroon). Figs 2, 3, 5 (photographs © S.A. Marshall), Fig. 4 (photograph © M. Reemer), Figs 6, 7 (photographs © A. Ssymank).

Ptilobactrum neavei Bezzi, 1915 (Fig. 167) and some other Microdontinae, or absent in some *Eristalinus* Rondani and *Syritta* Le Peletier & Serville (Fig. 174); parts of wing venation variable, such as cell r_1 open (Figs 122, 136, 137, 143, 146, 150) or closed (Figs 139, 140), vein R_{4+5} straight (Figs 130, 132, 158, 166, 172), moderately sinuate (Figs 129, 131) to strongly sinuate (Figs 127, 140, 148, 151, 153, 175), vein A_1 straight or curved, pterostigmal crossvein present (Fig. 165) or absent; wing membrane, including alula, virtually without microtrichia to entirely microtrichose; hyaline (Figs 125, 127, 129, 130, 166, 171, 178), with maculae (Figs 159, 169, 173), dark fascia (Fig. 144), to almost entirely darkened (Figs 121, 124, 126, 128, 151, 154, 155); calypter usually well-developed (Figs 180–182), except strongly reduced in *Spheginobaccha*. Legs simple to highly modified; hind coxa, trochanter and femur simple (Figs 190, 196, 197), or with modifications, such as



Figs 60.8–13. Photographs of living Afrotropical Syrphidae: (8) *Eumerus* sp. (Tanzania); (9) *Eupeodes corollae* (F.) (South Africa); (10) *Mesembrius* (*Mesembrius*) sp. (Tanzania); (11) *Metadon* sp. (South Africa); (12) *Monoceromyia* sp. (Cameroon); (13) *Phytomia incisa* (Wiedemann) (Kenya). Figs 8–10 (photographs © S.A. Marshall), Figs 11, 12 (photographs © A. Ssymank), Fig. 13 (photograph © M. Reemer).

spines (Figs 184, 194), spurs (Figs 187, 192), tubercles (Fig. 186) and/or ventrally expanded (Figs 188, 193); hind femur slender (Figs 190, 196, 197) or thickened (Figs 191, 194) to incrassate (Figs 192, 195); fore and hind femur and tibia sometimes modified; in some genera (e.g., *Mesembrius* Rondani) sexually dimorphic.

Abdomen variable in shape, from petiolate (constricted) (Figs 2, 201) to oval (Figs 198, 199) or very broad (Figs 82, 87); male terminalia (Figs 207–210) rotated, partly concealed beneath abdomen; in Eristalinae and Microdontinae male terminalia morphology often species-specific, but in Syrphinae less differentiated; female terminalia telescopic, weakly to moderately sclerotised (Fig. 211). In some genera (e.g., *Orthonevra* Macquart and *Sphaerophoria* Le Peletier & Serville) female terminalia have important taxonomic characters.

Due to mimicry, some Syrphidae may be easily confused in the field, but compared to other flies, they are distinctive and straightforward to recognise. Some Conopidae (see Chapter 66), Stratiomyidae (see Chapter 41) and Rhiniidae (see Chapter 115) are superficially similar, but Syrphidae can be distinguished by the absence of a ptilinal fissure (except present in *Ptilobactrum neavei*), a seta-like empodium between the tarsal claws, large basal wing cells *br*, *bm* and *cua*, closed cell *dm*, branches of vein M_1 turned up to run parallel to wing margin joining unbranched vein R_{4+5}, forming closed cell r_{4+5} and (except in a few species) the presence of a spurious vein (Fig. 120).

Biology and immature stages

Adult Syrphidae have a characteristic flight mode, which typically comprises remaining in one spot in the air, combined with rapid, darting flight, hence their vernacular name "hoverflies". Many species of the genus *Allobaccha* Curran, however, have broad wings and an exceptionally low wing beat, reminiscent of microlepidoptera. Some hoverflies mimic the flight behaviour of Hymenoptera, such as the rapid, zig-zag flight of *Graptomyza* and species of the tribe Cerioidini. Hovering is also known in some other Diptera families with representatives in the Afrotropical Region, including Curtonotidae (see Chapter 103), Pipunculidae (see Chapter 61) and Rhiniidae (see Chapter 115). Adult hoverflies often occur on flowers, where they feed on pollen and nectar, hence their alternative vernacular name "flower flies". Microdontinae adults rarely visit flowers and some species do not feed at all.

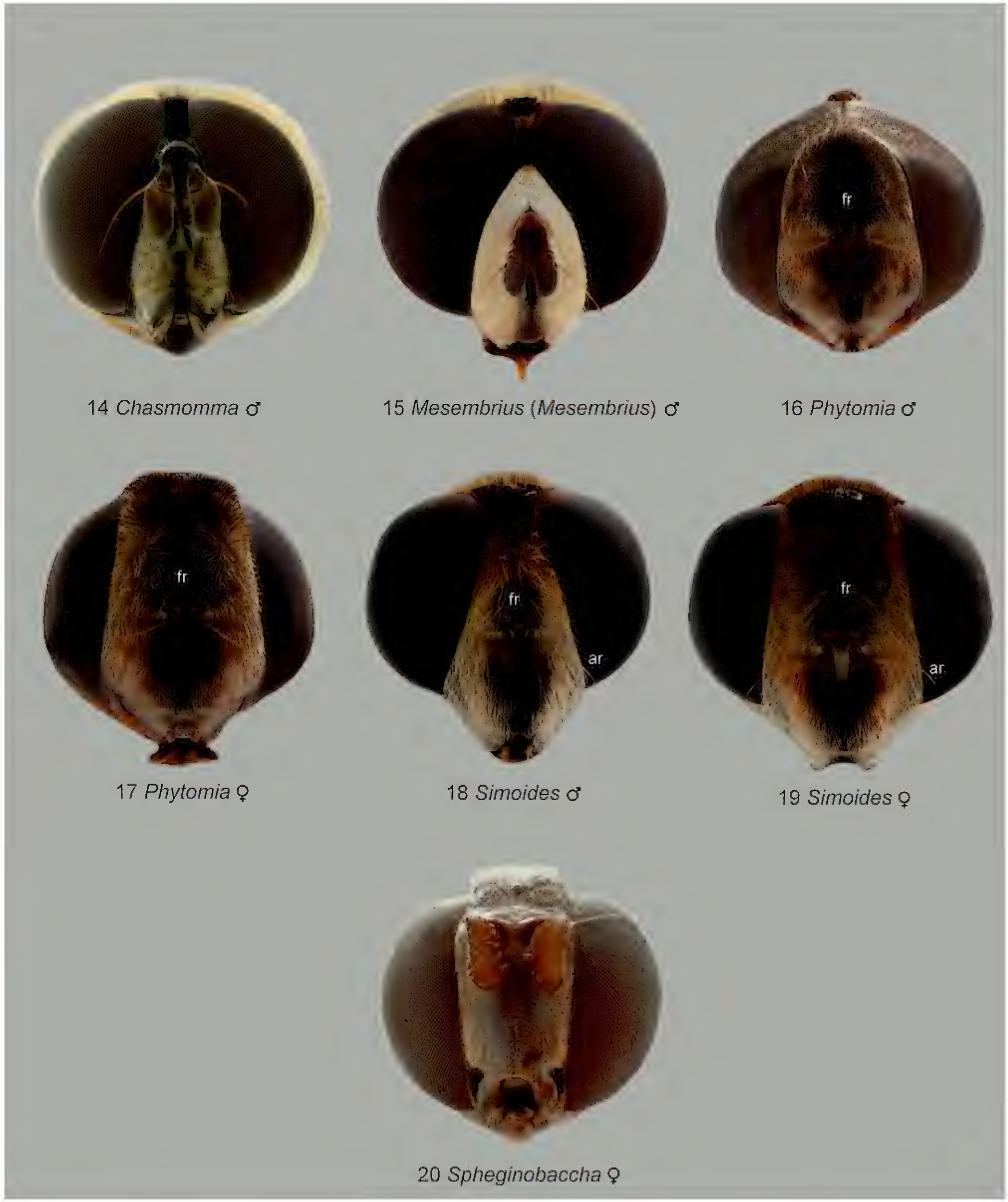
Syrphidae are typical Cyclorrhapha, with immature stages comprising the egg, three larval instars and the pupa (or pharate adult) contained within a puparium (the dried cuticle of the third-instar larva). An outstanding syrphid attribute, is the diversity of larval forms and biologies; so aside from larval biology being a subject in its own right, larvae represent a significant data source, enabling testing, support and supplement of taxonomic and systematic conclusions based on other character sets. The biology and immature stages of Afrotropical Syrphidae are, however, poorly known, other than a few notable exceptions, most information provided in this section is based on extralimital examples.

An extensive literature exists on syrphid larvae and the following publications provide an introduction: Dumbardon-Martial (2016); Fleischmann *et al*. (2016), Jordaens *et al*. (2015); Pérez-Lachaud *et al*. (2014); Reemer & Rotheray (2009); Rojo *et al*. (2003); Rotheray (1993); Rotheray & Gilbert (1999, 2011: 52); Rotheray *et al*. (2000); Ureña & Hanson (2010); Weng & Rotheray (2008) and Zuijen & Nishida (2011).

Eggs are deposited singly or in batches, usually in the vicinity of the larval breeding medium or development site. Fecundity is variable, with up to 326 eggs produced by a single female of *Helophilus trivittatus* (F., 1805) (non-Aftrotropical) in the field (F. Gilbert, pers. comm. 2019). In some taxa, the morphology of the chorion is species-specific (Chandler 1968; Kuznetsov & Yu 1988).

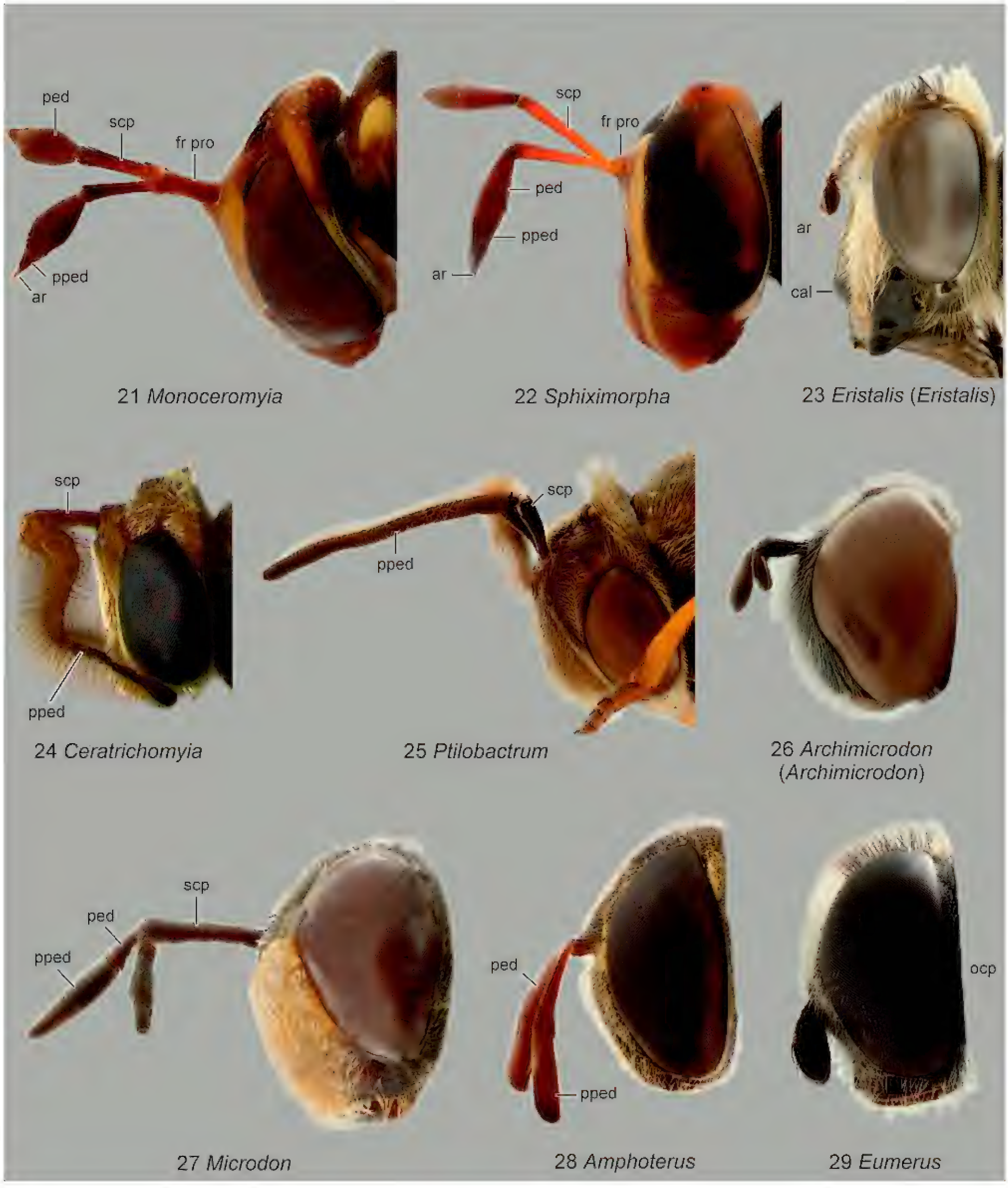
Microdontinae larvae (Figs 212, 216) develop within ants' nests and feed on the early stages of their ant hosts. Larvae of most Pipizinae and Syrphinae (Figs 214, 217) are predators of soft-bodied, colonial insects, such as aphids, scale insects, whiteflies, *etc.* (Hemiptera: Sternorrhyncha), with some species predatory on Thysanoptera, on larvae of Coleoptera and Lepidoptera, or even on adult Diptera (Rotheray & Gilbert 2011: 191). Larvae of Eristalinae (Figs 213, 218, 220–222), comprise a diverse range of phytophagous and saprophagous forms, including the distinctive and well-known long-tailed or "rat-tailed maggots" (Fig. 218). Eristalinae also includes occasional zoophages, such as certain larval *Volucella* Geoffroy (non-Afrotropical), where third-instars are facultative predators of dead or dying bees (Apidae) and wasps (Vespidae) (Rupp 1989). Phytophagous eristalines include a large and diverse group of Afrotropical *Eumerus* Meigen and *Merodon* Meigen species that develop in roots and bulbs, although some larvae in this group are saprophagous (Ricarte *et al*. 2008). Saprophagous forms are found in a vast array of decaying organic materials, from dung, exudations of plant sap or sap fluxes, to a wide range of waterbodies and aquatic habitats.

Four generalised larval forms are recognised. In larvae of Microdontinae the mouthhooks are blade-like, with serrated apical and ventral margins and are situated at the apex of the cephaloskeleton. Larvae (Figs 212, 216) are usually hemispherical, with a distinct lateral fringe and with the prothorax, mesothorax and mouthparts concealed in a ventral pocket of the metathorax, which consequently forms the anterior margin of the larva. The anal segment and posterior respiratory process are short. Larvae of Syrphinae (+ Pipizinae) (Figs 214, 217) have a beak-like apex to the cephaloskeleton with an elongated, thin and sclerotised labrum and labium. The stylet-like mouthhooks are incorporated into and support the side margins of the cephaloskeleton and play no independent role in feeding. Syrphine larvae usually occur on plants and are distinctive among Diptera larvae, in being cryptic and exhibiting a diverse range of colour patterns and associated behaviours. The anal segments and posterior respiratory processes are usually short (Fig. 214). Larvae of Eristalinae exhibit two generalised forms corresponding to phytophagy and saprophagy. The phytophagous forms (e.g., larvae of *Eumerus* and *Merodon*) have mouthhooks situated at the apex of the cephaloskeleton, which are hook-like and usually project from the mouth and a short anal segment and posterior respiratory process. The saprophagous forms (e.g., larvae of *Eristalis* Latreille and *Eristalinus*) have reduced mouthhooks that support a pot-like filter at the front of the cephaloskeleton and the anal segment is elongate and retractile to varying degrees (Fig. 213). Unlike



Figs 60.14–20. Heads of Syrphidae (frontal views): (14) *Chasmomma* sp. ♂; (15) *Mesembrius* (*Mesembrius*) sp. ♂; (16) *Phytomia* sp. ♂; (17) same ♀; (18) *Simoides* sp. ♂; (19) same ♀; (20) *Spheginobaccha* sp. ♀.

Abbreviations: ar – arista; fr – frons.



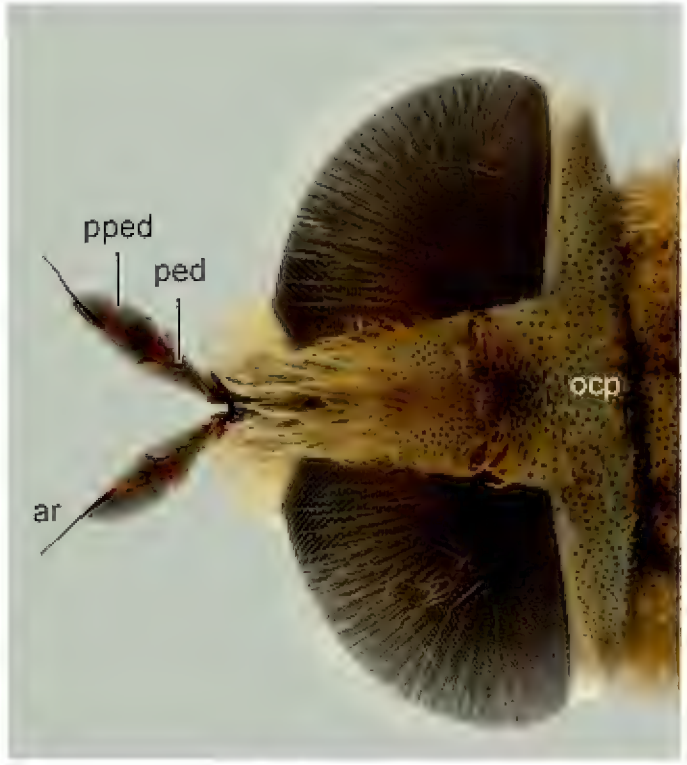
Figs 60.21–29. Heads of Syrphidae (lateral views): (21) *Monoceromyia* sp.; (22) *Sphiximorpha* sp.; (23) *Eristalis* (*Eristalis*) *tenax* (L.); (24) *Ceratrichomyia* sp.; (25) *Ptilobactrum neavei* Bezzi; (26) *Archimicrodon* (*Archimicrodon*) sp.; (27) *Microdon* (*Microdon erythros* species-group) sp.; (28) *Amphoterus braunsi* Doesburg; (29) *Eumerus* sp.

Abbreviations: ar – arista; cal – callus; fr pro – frontal prominence; ocp – occiput; ped – pedicel; pped – postpedicel; scp – scape.

microdontine and syrphine larvae, eristaline larvae usually possess prolegs with crochets.

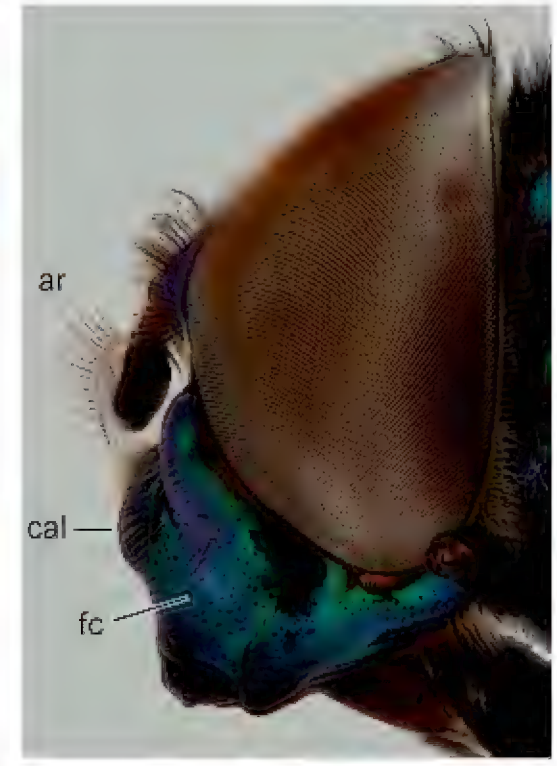
Syrphid larvae usually vacate their development sites and seek a drier place to pupariate. With the exception of most syrphines, a few days after formation of the puparium, respiratory "horns" appear from the anterior dorsal surface. These pupal horns are a source of useful taxonomic characters. Third-instar larvae (Figs 212–215, 220–222) and puparia (Figs 219, 223) can be recognised by the anal segment which, in most genera, has a single, sclerotised breathing tube, the position of the anus on the anteroventral margin of the anal segment and the prothorax with longitudinal grooves (Fig. 215). These grooves are, however, slight and less conspicuous in larvae of Microdontinae and Syrphinae.

Knowledge of immature stages of Afrotropical syrphids is very incomplete and most larvae remain to be discovered. Kaufmann (1973) obtained the larva of *Paragus* (*Afroparagus*) *borbonicus* Macquart, 1842 from aphids on cocoa leaves. Schmutterer (1972*a*, *b*, 1974) reared a large number of predatory Afrotropical syrphines, but did not describe the immature stages. Láska *et al*. (2000) described the puparium of *Afrosyrphus varipes* Curran, 1927 and Mazánek *et al*. (1999) described the puparia of several *Betasyrphus* Matsumura species. De Moor (1973) recorded larvae of *Eumerus obliquus* (F.,



30 *Megatrigon*

31 *Graptomyza*



32 *Ornidia*

33 *Paragus* (*Pandasyopthalmus*)

34 *Paragus* (*Afroparagus*)

35 *Paragus* (*Serratoparagus*)

Figs 60.30–35. Heads of Syrphidae: (30) *Megatrigon* sp., dorsal view; (31) *Graptomyza* sp., dorsolateral view; (32) *Ornidia obesa* (F.), lateral view; (33) same, *Paragus* (*Pandasyopthalmus*) sp.; (34) same, *P.* (*Afroparagus*) sp.; (35) same, *P.* (*Afroparagus*) *borbonicus* Macquart.

Abbreviations: ar – arista; cal – callus; fc – face; ocp – occiput; ped – pedicel; pped – postpedicel.

1805) in decaying fruits and the roots of potted plants and Ricarte *et al*. (2008) reared the larvae of this species on decaying *Opuntia* (Cactaceae) from Mallorca, Spain and described larval morphology in detail. Copeland *et al*. (1999) discovered the larvae of *Senaspis haemorrhoa* (Gerstaecker, 1871) in a water-filled pocket of an elephant damaged, cycad stump, *Encephalartos tegulaneus* Melville (Zamiaceae) in Kenya and described the puparium. Whittington (1994*a*) described the larvae of two Afrotropical and one non-Afrotropical *Graptomyza* species from decaying fruits. Whittington & Rotheray (1997) described the larvae of the introduced *Ornidia obesa* (F., 1775) and details of the larval morphology of this species were also provided by Rotheray *et al*. (2005).

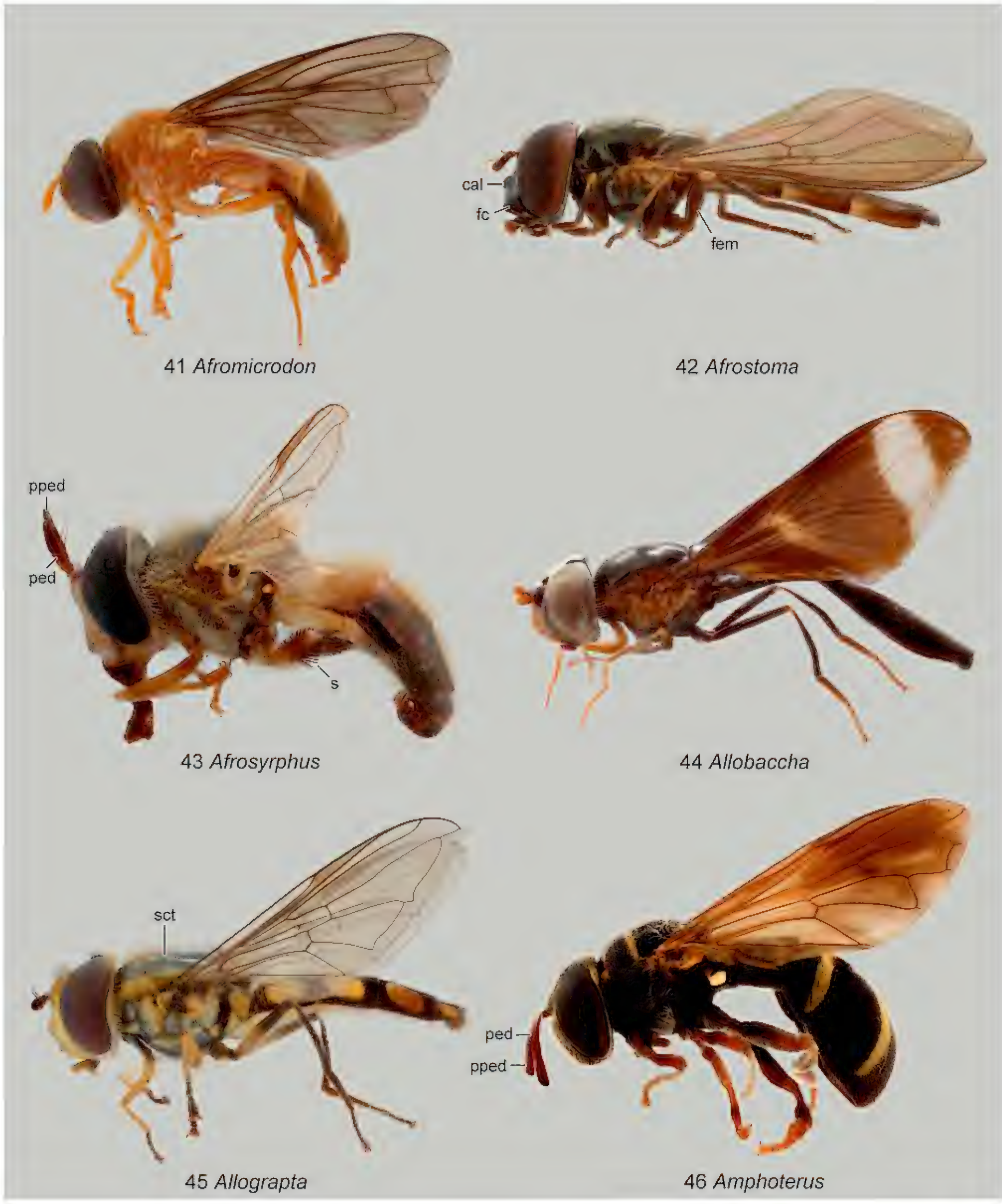
Perhaps the greatest gap in our knowledge is that of the early stages of the Microdontinae. Globally, all known larvae develop in association with ant colonies, either as predators or ectoparasitoids of the immature stages (Pérez-Lachaud *et al*. 2014; Reemer 2013). Very few Afrotropical records of larvae of this subfamily are known (Reemer 2013). In South Africa, two species of *Paramixogaster* Brunetti were reared from ants' nests of the genera *Crematogaster* Lund and *Lepisiota* Santschi (Formicidae) (Speiser 1913) and an unidentified microdontine larva was found in Tanzania in a nest of *Tetraponera* Smith ants in an *"Acacia"* thorn gall (Hocking 1970). It will be especially interesting to discover the biology and larval habits of *Sphegino-baccha* (Fig. 95), the sister-group of all other Microdontinae (Reemer & Ståhls 2013*a*), for understanding the development of myrmecophily in this subfamily (Reemer & Ståhls 2013*a*, *b*; Rotheray & Gilbert 2011: 188).

Economic significance

In their roles as pollinators, predators or decomposers, syrphids provide significant ecosystem services (Inouye *et al*. 2015; Ssymank *et al*. 2009: 39–49, 159–162). For example, flower visiting by adults is typical and in feeding on pollen and nectar they are assumed to be important pollinators, although their significance in this critical function requires better understanding (Rader *et al*. 2015; Rotheray & Gilbert 2011: 178; Ssymank *et al*. 2009: 59–162). Species with a short proboscis tend to visit a wider range of flowers than do those with a longer proboscis (*e.g.*, *Asarkina* (Fig. 50) and *Rhingia* (Fig. 91)), that exploit flowers with deep corollas (but see Vlašánková *et al*. (2017), for an alternative scenario). Feeding preferences vary from a few plant

Figs 60.36–40. Heads and antennae of Syrphidae: (36) head of *Afrostoma quadripunctatum* Skevington, Thompson & Vockeroth, lateral view; (37) same, *Melanostoma* sp.; (38) same, *Toxomerus floralis* (F.); (39) antennae of *Phytomia* sp., frontal view; (40) same, *Senaspis* sp.

Abbreviations: ar – arista; cal – callus; ped – pedicel; pped – postpedicel; scp – scape.



41 *Afromicrodon* 42 *Afrostoma*

43 *Afrosyrphus* 44 *Allobaccha*

45 *Allograpta* 46 *Amphoterus*

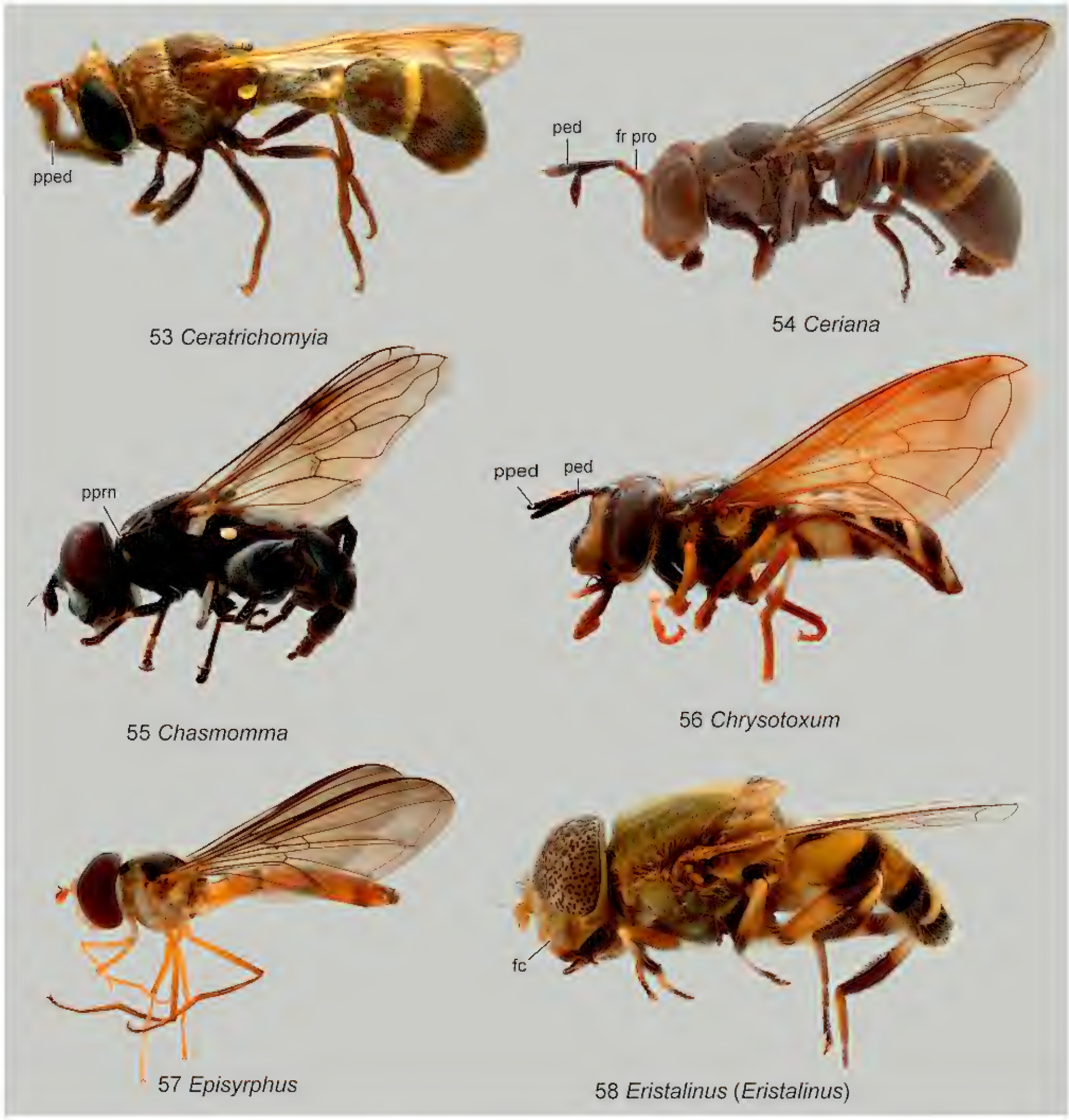
Figs 60.41–46. Habitus of Syrphidae (lateral views): (41) *Afromicrodon* sp.; (42) *Afrostoma quadripunctatum* Skevington, Thompson & Vockeroth; (43) *Afrosyrphus varipes* Curran; (44) *Allobaccha* sp.; (45) *Allograpta* sp.; (46) *Amphoterus braunsi* Doesburg.

Abbreviations: cal – callus; fc – face; fem – femur; ped – pedicel; pped – postpedicel; s – setae; sct – scutum.

Figs 60.47–52. Habitus of Syrphidae (lateral views): (47) *Anasimyia* sp.; (48) *Archimicrodon* (*Hovamicrodon*) sp.; (49) *Archimicrodon* (*Archimicrodon*) sp.; (50) *Asarkina* (*Asarkina*) sp.; (51) *Betasyrphus* sp.; (52) *Calcaretropidia* sp.

Abbreviations: fc – face; ped – pedicel; pped – postpedicel.

species (oligolectic) to a great array of different flowers (polylectic). Predatory syrphine larvae are valuable control agents of plant pests on agricultural crops (e.g., Amorós-Jiménez *et al*. 2015; Bergh & Short 2008; Bugg *et al*. 2008; Eckberg *et al*. 2015; Greco 1998; Nelson *et al*. 2012; Pineda & Marcos-García 2008; Schmidt *et al*. 2004; Tenhumberg & Poehling 1995). Saprophagous larvae are decomposers of organic matter (Martínez-Falcón *et al*. 2012; Rotheray *et al*. 2009) and species of several genera (e.g., *Eristalinus*, *Eristalis* and *Ornidia*, have been used to recycle agricultural wastes (Rotheray & Gilbert 2011: 200)). In contrast



53 *Ceratrichomyia*

54 *Ceriana*

55 *Chasmomma*

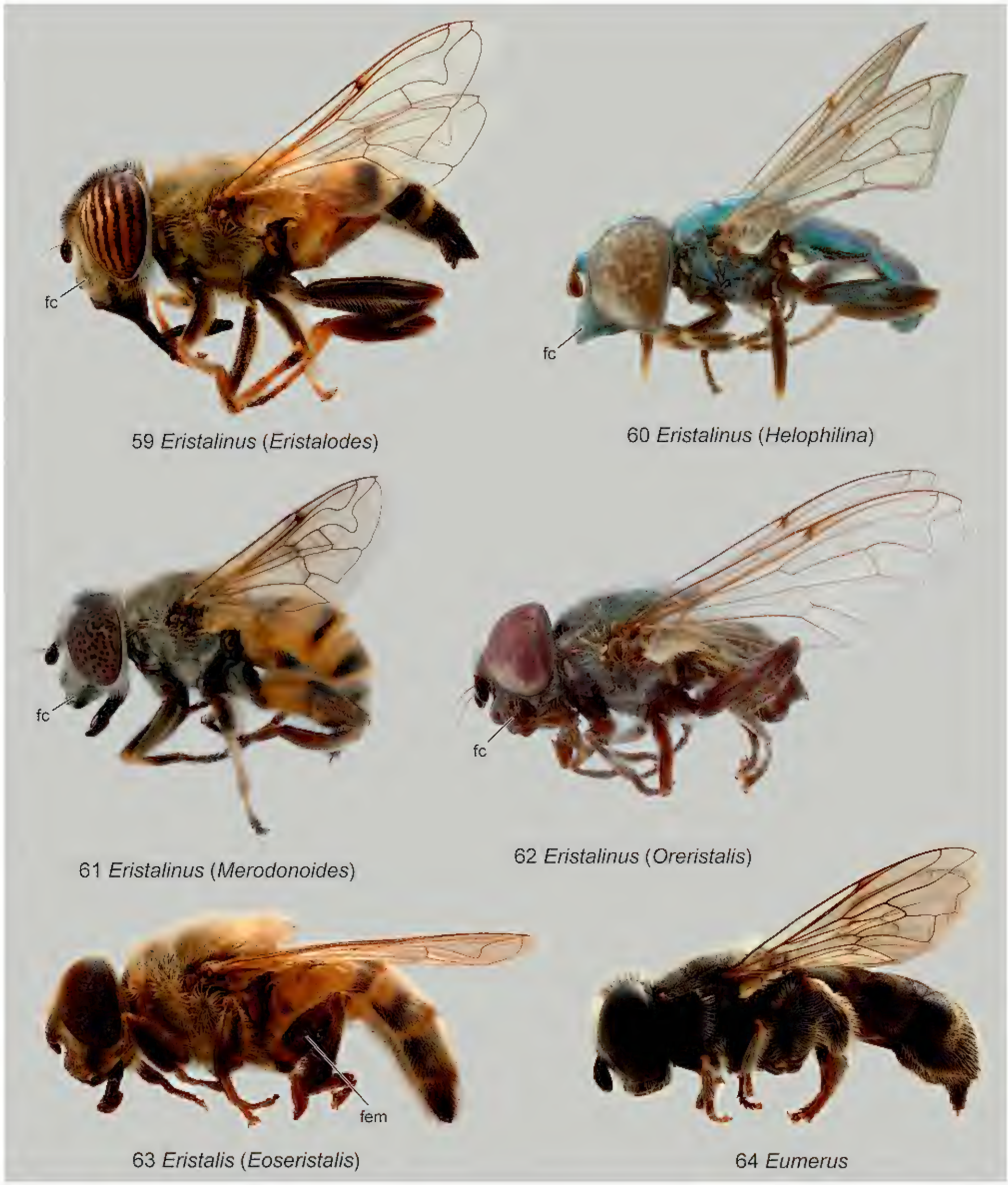
56 *Chrysotoxum*

57 *Episyrphus*

58 *Eristalinus* (*Eristalinus*)

Figs 60.53–58. Habitus of Syrphidae (lateral views): (53) *Ceratrichomyia* sp.; (54) *Ceriana* sp.; (55) *Chasmomma* sp.; (56) *Chrysotoxum continum* Bezzi; (57) *Episyrphus petilis* Vockeroth; (58) *Eristalinus* (*Eristalinus*) sp.

Abbreviations: fc – face; fr pro – frontal prominence; ped – pedicel; pped – postpedicel; pprn – postpronotum.



Figs 60.59–64. Habitus of Syrphidae (lateral views): (59) *Eristalinus* (*Eristalodes*) sp.; (60) *Eristalinus* (*Helophilina*) *smaragdinus* Macquart; (61) *Eristalinus* (*Merodonoides*) *modestus* (Wiedemann); (62) *Eristalinus* (*Oreristalis*) sp.; (63) *Eristalis* (*Eoseristalis*) sp.; (64) *Eumerus* sp.

Abbreviations: fc – face; fem – femur.

to these benefits, the phytophagous larvae of several species of the genera *Eumerus* and *Merodon* are occasional pests of ornamental flowers (Ricarte *et al*. 2008) and accidental myiasis is known in species of Eristalinae (Aguilera *et al*. 1999).

Classification

Approximately 6,200 species in 210 genera of Syrphidae have been described globally (Pape & Evenhuis 2019), with the highest species diversity in the Neotropical Region (Thompson 2019*a*). Within the Afrotropical Region (see Fig. 1.1 in Kirk-Spriggs 2017: 3) *ca* 610 species in 60 genera are known. In the past few years, however, dozens of new Afrotropical species have been discovered and await description.

Syrphidae are ascribed to the brachyceran clade Cyclorrhapha. The first-branching lineages of the Cyclorrhapha (= "Aschiza") are included in two superfamilies, Phoroidea (Phoridae, Lonchopteridae, Platypezidae and the non-Afrotropical families Ironomyiidae and Opetiidae) and Syrphoidea (Syrphidae). The small parasitic family Pipunculidae (big-headed flies), have traditionally been considered sister-group to Syrphidae (*e.g.*, Cumming *et al*. 1995; McAlpine 1989: 1424) and placed within the Syrphoidea (Rotheray & Gilbert 2008). Molecular datasets, however, invariably place the pipunculids as sister to Schizophora (Wiegmann *et al*. 2011; Young *et al*. 2016), which is also supported by some morphological data (Tachi 2014).

Currently, four subfamilies are recognised within the Syrphidae: Eristalinae, Microdontinae, Pipizinae and Syrphinae (*e.g.*, Mengual *et al*. 2015). Pipizinae does not occur in the Afrotropical Region and molecular data suggests that Eristalinae monophyly is not supported (*e.g.*, Pauli *et al*. 2018; Young *et al*. 2016). Tribal division of the family is based largely on morphological characters and larval biology (Thompson & Rotheray 1998: 88). A total of 15 tribes are recognised, but the classification into tribes has not been generally accepted and the relationships among them have only been studied recently (Young *et al*. 2016). Some of the genera have been placed in different tribes and some tribes have even been placed in different subfamilies.

Microdontinae is a subfamily with two tribes: Microdontini and Spheginobacchini. All known larvae develop in association with ant colonies, where they feed on the early stages of their hosts, but the ecology and larval biology of most microdontine groups remain unknown. The tribe Spheginobacchini has, at times, been placed within the subfamilies Eristalinae, Syrphinae and Pipizinae (as "Pipizini"), but its placement in the Microdontinae is now generally accepted (Mengual *et al*. 2015; Reemer & Ståhls 2013*b*; Rotheray & Gilbert 2011: 92; Ståhls *et al*. 2003).

The paraphyletic Eristalinae is a large subfamily with nine tribes: Brachyopini, Callicerini, Cerioidini, Eristalini, Merodontini, Milesiini, Rhingiini, Sericomyiini and Volucellinini, of which only Callicerini and Sericomyiini do not occur in the Afrotropical Region. It is the subfamily with the highest number of species and larval biology diversity. Brachyopini are not supported by the latest phylogenetic studies and the placement of Callicerini, Merodontini and Volucellini within the subfamily remains uncertain or unresolved (Hippa & Ståhls 2005; Mengual *et al*. 2008, 2012, 2015). Merodontini was resolved as sister-group to the other Eristalinae + Syrphinae + Pipizinae and Volucellini and *Helophilus* Meigen (non-Afrotropical) were recorvered in different nodes, with the other included eristaline tribes forming a clade, *i.e.*, Rhingiini, *Sphegina* Meigen (Brachyopini), Callicerini (non-Afrotropical) and Milesiini. However, a larger and broader taxon sampling is required.

Syrphinae is also a large subfamily with four tribes: Bacchini, Paragini, Syrphini and Toxomerini. Bacchini and Toxomerini are not supported by the latest phylogenetic studies and the position of Paragini remains uncertain. Syrphinae and Pipizinae are reciprocally monophyletic and sister-groups to each other. This implies that predatory larvae feeding on soft-bodied arthropods have evolved only once in the evolution of the Syrphidae. The current tribal classification within Syrphinae is not supported in concordance with the last phylogenetic studies (Mengual *et al*. 2008, 2015; Rotheray & Gilbert 1999; Ståhls *et al*. 2003). Bacchini was recovered as paraphyletic and its representatives (*Melanostoma* Shiner and two non-Afrotropical genera: *Platycheirus* Le Peletier & Serville and *Baccha* F.), were resolved in two groups, which is partly in agreement of previous studies (Mengual *et al*. 2008, 2015; Ståhls *et al*. 2003).

Identification

The first comprehensive revision of Afrotropical Syrphidae was the work of Bezzi (1915). He studied the collection of the Imperial Bureau of Entomology at the British Museum (Natural History) (now the Natural History Museum, London). This monograph included an identification key to the 27 genera of Afrotropical Syrphidae then known and listed 249 species. Subsequently, a number of generic identification keys have been published, but all of these are incomplete and out of date with respect to the Afrotropics, namely: Curran (1927) (27 Afrotropical genera); Hull (1949) (31 genera); Thompson & Rotheray (1998: 93) (33 genera); Vockeroth (1969) (nine genera of the subfamily Syrphinae) and Vockeroth & Thompson (1987: 718) (24 genera). More recently, Thompson & Skevington (2014) published an identification key to genera of Afrotropical Syrphinae (on which the identification key below is based) and Reemer & Ståhls (2013a) published an identification key to the genera of the Microdontinae of the world.

Published papers that include identification keys to species include the series published by Curran (1927, 1938*a*, *b*, 1939*a*, *b*) and this series remains the basis for much current and ongoing taxonomic revision. Smith & Vockeroth (1980) published the first catalogue of Afrotropical Syrphidae, which listed 470 species in 55 genera. Dirickx (1998) updated this catalogue and listed 522 species in 54 genera and provided distribution maps for 73 species. These catalogues do not include identification keys, but indicate progress that has been made in the taxonomy of Syrphidae and illustrate the uncertain taxonomic status of many genera and species. Moreover, there are dozens of new species to be described. Whittington (2003) provided an assessment of current taxonomic and faunistic knowledge of the fauna.

65 *Eupeodes*

66 *Sphaerophoria* (*Exallandra*)

67 *Graptomyza*

68 *Ischiodon*

69 *Sphaerophoria* (*Loveridgeana*)

70 *Lyneborgymyia*

Figs 60.65–70. Habitus of Syrphidae (lateral views): (65) *Eupeodes corollae* (F.); (66) *Sphaerophoria* (*Exallandra*) *cinctifacies* (Speiser); (67) *Graptomyza* sp.; (68) *Ischiodon aegyptius* (Wiedemann); (69) *Sphaerophoria* (*Loveridgeana*) *beattiei* Doesburg & Doesburg; (70) *Lyneborgymyia magnifica* Doczkal & Pape. Fig. 70 (after Doczkal & Pape 2009, fig. 1).

Abbreviations: cal – callus; fc – face; sct – scutum.

Terminology for adult morphology applied follows Cumming & Wood (2017), but one important thoracical character in Syrphidae (not illustrated in Cumming & Wood 2017)), is the "metasternum", which is the sclerite ventral to the meron between coxae 2 and 3 (Fig. 112) (for a discussion on the terminology of this sclerite we refer to Thompson 1999). In the "Synopsis of the fauna" section below the following relative body size classes are applied: small-sized (body length: < 9 mm), medium-sized (9–14.5 mm) and large-sized (> 14.5 mm).

Afrotropical syrphid larvae are too poorly known to provide an identification key, but details of the known biology of larvae is included in "Synopsis of the fauna" section below and general information on syrphid larvae is provided by Rotheray (1993 and references therein). Since completion of this chapter, Mengual *et al*. (2021) revised the genus *Sphaerophoria*, and assigned the Afrotropical species two subgenera: *S*. (*Exallandra*) with two species; and *S*. (*Loveridgeana*) with three species. These changes are adopted in the below identification key, but not in the "Synopsis of the fauna" section.

Adult Syrphidae are usually collected in vials or killing jars in the field. Larger specimens are direct-pinned and smaller specimens are micro-pinned for later double-mounting (see Chapter 2).

Key to genera of Afrotropical Syrphidae

1. Thorax with postpronotum setulose (e.g., Fig. 103); head not strongly concave posteriorly, postpronotum clearly exposed (e.g., Figs 55, 76); male abdomen with segment 5 not visible in dorsal view (e.g., Fig. 198) (ERISTALINAE and most MICRODONTINAE [in part]) 2

– Thorax with postpronotum bare (e.g., Fig. 104); head strongly concave posteriorly, closely appressed to thorax, so postpronotum partly or entirely obscured (e.g., Figs 42, 50); male abdomen with segment 5 usually visible in dorsal view, varying in form of subquadrate or subtriangular, to short transverse sclerite (e.g., Fig. 199); if male abdomen with segment 5 not visible, then antennae longer than head (some *Ceratrichomyia*, Fig. 53 and *Paramixogaster*, Fig. 85) (SYRPHINAE and some MICRODONTINAE [in part]) 58

2. Antenna with terminal thickened apical stylus-like arista (e.g., Figs 21, 22) 3

– Antenna with dorsal or sublateral arista, never inserted apically; arista thin and basal (e.g., Figs 28–40) 6

3. Thorax with postmetacoxal bridge posterior to hind coxae (Fig. 113); metathoracic pleuron either entirely fused or adjacent posterior to hind coxae . . . . . *Polybiomyia* Shannon

– Thorax without postmetacoxal bridge, broadly membranous posterior to hind coxae; metathoracic pleura widely separated 4

4. Head without frontal prominence or if present, then this very short, < ½ as long as antennal pedicel (Figs 22, 96) . . . . . *Sphiximorpha* Rondani

– Head with frontal prominence at least as long as antennal pedicel (e.g., Figs 12, 21, 54, 80) 5

5. Abdomen not petiolate, with abdominal segment 2 as broad as abdominal segment 1 (Fig. 200) . . . . . *Ceriana* Rafinesque

– Abdomen distinctly petiolate, with abdominal segment 2 much narrower than abdominal segments 1 and 3 (Fig. 201) . . . . . *Monoceromyia* Shannon

6. Wing vein R_{4+5} moderately (e.g., Fig. 134) to strongly (e.g., Figs 138–140) sinuate; crossvein *r–m* positioned at most at distal ⅓ of cell *dm* (e.g., Fig. 141) 7

– Wing vein R_{4+5} straight (e.g., Fig. 126) or virtually so (e.g., Fig. 131), if strongly sinuate, then crossvein *r–m* positioned at distal ⅕ of cell *dm* (e.g., Fig. 156) 30

7. Wing cell r_1 open (as in Fig. 141), if closed than not markedly petiolate (e.g., Fig. 148) 8

– Wing cell r_1 closed and markedly petiolate (e.g., Figs 139, 140) 18

8. Wing vein M_1 markedly recessive distally (e.g., Figs 147, 151) 9

– Wing vein M_1 processive distally (e.g., Figs 134, 138–140) 10

9. Male wing cell r_{4+5} divided by auxiliary vein between veins R_{4+5} and M_1 (Fig. 147); female with incomplete vein between veins R_{4+5} and M_1; legs without apicoventral triangular expansion on anterior side of hind femur. . . . . *Lyneborgimyia* Doczkal & Pape

– Male and female wing cell r_{4+5} without auxiliary vein between veins R_{4+5} and M_1 (Fig. 151); legs with apicoventral triangular expansion on anterior side of hind femur (Fig. 188) . . . . . *Merodon* Meigen

10. Apical margin of scutellum with flattened rim (e.g., Fig. 105); legs with (e.g., Fig. 184) or without spines on hind coxa 11

– Apical margin of scutellum without flattened rim; all legs without spines on hind coxa 12

11. Abdomen broadly oval; male legs without spurs on hind coxa; hind femur distinctly swollen (Fig. 183), with anterolateral patch of setulae . . . . . *Mallota* Meigen [in part; *M. aperta* (Bezzi, 1912)]

– Abdomen elongate; male legs with long ventral spurs on hind coxa (Fig. 184); hind femur only slightly enlarged, without anterolateral patch of setulae (Fig. 184) . . . . . *Syrittosyrphus* Hull

12. Compound eye setulose; thorax with katepimeron bare. . . . . *Mallota* Meigen [in part]

– Compound eye bare (e.g., Figs 14, 15); katepimeron bare or setulose 13

13. Thorax with katepimeron conspicuously setulose; hind tarsomere 1 with basoventral globuliferous setae (Fig. 189); male eyes holoptic (Fig. 15). . . . . *Mesembrius* Rondani 14

– Thorax with katepimeron bare, or with very few inconspicuous setulae; mid tarsomere 1 without basoventral globuliferous setae; male eyes holoptic or dichoptic (e.g., Fig. 14) 15

14. Scutum with pale pruinescent longitudinal vittae (Figs 10, 76); male terminalia never greatly enlarged (Fig. 202) (widespread Afrotropical Region) . . . . . .*Mesembrius sensu stricto*

– Scutum without pruinescent longitudinal vittae; male terminalia usually greatly enlarged (Fig. 203) (confined to Madagascar) . . . . . *Mesembrius* (*Vadonimyia* Séguy)

15. Wing vein R_{4+5} moderately sinuate (Fig. 134); male eyes dichoptic (Fig. 14) . . . . . *Chasmomma* Bezzi

– Wing vein R_{4+5} strongly sinuate (e.g., Fig. 127); male eyes holoptic or dichoptic. 16

16. Head with carinate face conically produced below (Fig. 47); male eyes dichoptic; wing membrane entirely microtrichose; thorax with postalar setulae tuft (as in Fig. 117). . . . . .*Anasimyia* Schiner

– Head with face tuberculate (as in Fig. 71); male eyes holoptic; wing membrane partially bare in basal ⅓ (e.g., Fig. 169); thorax without postalar setulae tuft 17

17. Thorax with dorsomedial (triangular) part of anepimeron setulose; hind femur massive, greatly thickened; fore and hind tibiae orange-brown with orange-red setulae (confined to Madagascar) . . . . . .*Mallota* Meigen [in part; *M. meromacrimima* Hull, 1941]

– Thorax with dorsomedial (triangular) part of anepimeron bare; hind femur not greatly thickened, but dilated apically (Fig. 185); all legs with tibiae dark with dark setulae (Democratic Republic of Congo) . . . . . .*Senaspis* Macquart [in part; *S. pennata* (Hervé-Bazin, 1914)]

18. Thorax with setulae on triangular part of anepimeron as long as that on anterior part of anepimeron (Fig. 106). . . . . .*Eristalinus* Rondani 19

– Thorax with triangular part of anepimeron bare, or with setulae much shorter than that on anterior part of anepimeron (e.g., Fig. 107) 23

19. Small (< 7 mm), metallic green species (Fig. 60); wing membrane densely, uniformly microtrichose in apical ½ (Fig. 139); face strongly conical ventrally (Fig. 60); male eyes dichoptic . . . . . *Eristalinus* (*Helophilina* Becker)

– Larger (> 10 mm) metallic bluish to green or brownish to black species; wing membrane bare or sparsely microtrichose (e.g., Fig. 138); face rounded (e.g., Figs 58, 59, 62) or produced below (e.g., Fig. 61); male eyes dichoptic or holoptic 20

20. Compound eye bare or finely setulose dorsally, with ommatrichia no longer than ommatidial diameter; eyes maculate (Fig. 61); hind femur thickened, distinctly arcuate (Figs 61, 191); hind tibia strongly compressed, carinate in basoventral ⅓ (Fig. 191); male hind trochanter with ventral patch of short, stiff, black setulae . . . . . *Eristalinus* (*Merodonoides* Curran)

– Compound eye usually densely pilose, with ommatrichia much longer than ommatidial diameter; eyes maculate (e.g., Figs 7, 58, 62) or fasciate and maculate (e.g., Fig. 59) (eye pattern may be indiscernible in older museum specimens); hind femur at most slightly thickened, not arcuate (e.g., Fig. 190); hind tibia not compressed, nor carinate in basoventral ⅓ (e.g., Fig. 190); male hind trochanter without ventral patch of short, stiff, black setulae 21

21. Compound eye fasciate and maculate (Fig. 59) . . . . . *Eristalinus* (*Eristalodes* Mik)

– Compound eye maculate (e.g., Figs 7, 58, 62) 22

22. Brilliant metallic bluish to green flies; thorax with shiny mesonotum, without pruinescent maculae (Fig. 62). . . . . *Eristalinus* (*Oreristalis* Séguy)

– Colour not as above (Figs 7, 58), if metallic bluish to green, then thorax with pruinescent maculae on mesonotum . . . . . *Eristalinus sensu stricto*

23. Thorax with katepimeron setulose 24

– Thorax with katepimeron bare 27

24. Compound eye setulose (Fig. 23); antennal arista pubescent (Fig. 23); thorax with meron bare posteroventrally, without setulae anterior or ventral to posterior thoracic spiracle . . . . . *Eristalis* Latreille [in part; *E. tenax* (L., 1758)]

– Compound eye bare; antennal arista bare or pubescent; thorax with meron setulose posteroventrally, with or without setulae anterior or ventral to spiracle 25

25. Antennal arista bare (Fig. 40); wing membrane microtrichose on apical ½ (Fig. 169); posterior thoracic spiracle without long setulae on posterodorsal margin; male eyes holoptic . . . . . *Senaspis* Macquart [in part]

– Antennal arista pubescent (e.g., Fig. 39), with short to moderately long microtrichia, if arista bare, then wing membrane entirely bare [*Phytomia erratica* Bezzi, (1912)], at least apicoposteriorly (e.g., Figs 164, 170); thorax with precallar depression with numerous stiff setulae posteriorly; posterior thoracic spiracle with long setae on posterodorsal margin; male eyes holoptic or dichoptic. 26

26. Head with frons strongly rugose and shiny, usually with large bare area dorsal to antenna (Figs 16, 17); male eyes holoptic (Fig. 16) . . . . . *Phytomia* Guérin-Méneville

– Head with frons smooth, without large bare rugose area above antennae (smaller rugose area or enlarged lunule usually clothed in long setulae may be present) (Figs 18, 19); male eyes dichoptic (Fig. 18). . . . . *Simoides* Loew

27. Compound eye bare; male hind femur enlarged, with basolateral tubercle (Fig. 186), with distinct basolateral patch of black setulae . . . . . *Senaspis* Macquart [in part; *S. apophysata* (Bezzi, 1915)]

– Compound eye setulose; male hind femur enlarged or not, without basolateral tubercle, without distinct basolateral patch of black setulae 28

28. Hind tibia neither compressed nor carinate; wing membrane bare apically (Fig. 140). . . . . *Eristalis* Latreille [in part; *E.* (*Eoseristalis* Kanervo)]

– Hind tibia compressed and carinate in basoventral ⅓; wing membrane usually microtrichose in apical ⅓ or more 29

29. Hind femur not greatly swollen (Fig. 63); wing cell r_1 not bulbous apically (Fig. 140); male eyes holoptic . . . . . *Eristalis* Latreille [in part; *E. plumipes* Bezzi, 1912]

– Hind femur greatly swollen (Fig. 75); wing cell r_1 bulbous apically (Fig. 152); male eyes dichoptic . . . . . *Meromacroides* Curran

30. Head with face produced into long "snout", without callus (Fig. 91); antennal arista bare; eye bare; costal wing vein (C) and vein R_{4+5} ending well posterior to wing apex (Fig. 168) . . . . . *Rhingia* Scopoli 31

– Head with face not produced into "snout"; with or without callus; antennal arista bare, plumose or pectinate; eye bare or setulose; costal wing vein (C) and vein R_{4+5} ending anterior to wing apex (e.g., Fig. 154) 32

31. Male eyes dichoptic. . . . . *Rhingia* (*Eorhingia* Hull)

– Male eyes holoptic. . . . . *Rhingia sensu stricto*

32. Antennal arista plumose or pectinate, with branches at least 2 × as long as basal diameter of arista; compound eye setulose (e.g., Fig. 32); thorax with setae (e.g., Fig. 109); scutellum with shallow to deep medial depression (e.g., Fig. 109). 33

– Antennal arista bare; compound eye bare (e.g., Fig. 26) or setulose (e.g., Fig. 30); thorax without setae; scutellum convex, without medial depression (e.g., Figs 108, 110) 34

33. Head with face with single medial callus (Fig. 31); thorax with posterior anepimeron and katepimeron bare; notopleuron simple, not enlarged, scutellum with deep medial rounded depression (Fig. 109); wing cell r_1 open (Fig. 144); male eyes dichoptic . . . . . *Graptomyza* Wiedemann

– Head with face with 1 medial and 2 lateral calli (Fig. 32); thorax with posterior anepimeron and katepimeron setulose; notopleuron enlarged, produced posteriorly, scutellum with shallow depression before hind margin; wing cell r_1 closed and petiolate (Fig. 159); male eyes holoptic. . . . . *Ornidia* Le Peletier & Serville

34. Antenna usually elongate (but barely so in some *Afromicrodon* Thompson); scape and usually postpedicel > 2.5 × as long as wide (e.g., Fig. 27); eye bare; thorax with postmetacoxal bridge narrow, but complete; anterior anepisternum with flattened part setulose; wing vein R_{4+5} often with auxiliary vein in cell r_{4+5} (e.g., Figs 128, 132); cell r_1 open (e.g., Fig. 128). 35

– Antenna usually short; scape usually at most 2 × as long as wide, if more than 2 × as long, then eye pilose (*Amphoterus* Bezzi), then postpedicel usually rounded or oval (e.g., Fig. 29); thorax without

postmetacoxal bridge; anterior anepisternum setulose or bare; wing vein R_{4+5} usually without auxiliary vein in cell r_{4+5}; cell r_1 open or closed (e.g., Fig. 141) 45

35. Wing vein R_{4+5} without auxiliary vein in cell r_{4+5} (Fig. 121) . . . . . .*Afromicrodon* Thompson

– Wing vein R_{4+5} with auxiliary vein in cell r_{4+5} (e.g., Figs 128, 132). 36

36. Abdomen constricted (Fig. 53), petiolate, with abdominal tergite 2 narrower than tergite 3, or abdominal segment 2 clearly dorsoventrally flattened in lateral view . . . . . .*Ceratrichomyia* Séguy [in part; *C. behara* Séguy, 1951 & *C. bullabucca* Reemer, 2013]

– Abdomen not constricted (e.g., Fig. 77); abdominal tergite 2 as wide as, or wider than, tergite 3 . . . 37

37. Thorax with anepisternum entirely setulose, at most with small bare patch ventrally. 38

– Thorax with anepisternum extensively bare ventromedially, with bare patch reaching dorsally to at least ½ height of anepisternum 39

38. Antennal postpedicel bare in both sexes, shorter than or as long as scape (Fig. 77) . . . *Metadon* Reemer

– Antennal postpedicel with long setulae in male, 5 × as long as scape (Fig. 25) . . . . *Ptilobactrum* Bezzi

39. Antenna shorter than distance between antennal sockets and anterior oral margin (Figs 26, 48) . . . . . *Archimicrodon* Hull 40

– Antenna as long as, or longer than, distance between antennal sockets and anterior oral margin . . . . . .*Microdon* Meigen 41

40. Thorax with scutellar processes spoon-shaped (Fig. 110) . . . . . .*Archimicrodon* (*Hovamicrodon* Keiser)

– Thorax with scutellar processes blunt, sharp or absent. . . . . *Archimicrodon sensu lato*

41. Abdomen entirely yellowish red. . . . . .*Microdon* Meigen [in part; *M. erythros*-group]

– Abdomen not entirely yellowish red. 42

42. Antennal postpedicel significantly longer than scape . . . . . *Microdon* (*Myiacerapis* Hull)

– Antennal postpedicel shorter than scape 43

43. Hind tarsomere 1 long, strongly swollen, longer than apical 4 tarsomeres combined, in lateral view > 2 × as broad as hind tibia (Fig. 78) . . . . . .*Microdon* Meigen [in part; *M. tarsalis*-group]

– Hind tarsomere 1 short, less swollen, shorter than apical 4 tarsomeres combined, in lateral view < 2 × as broad as hind tibia. 44

44. Hind tarsomere 1 without dorsal groove . . . . . .*Microdon* Meigen *sensu stricto* [in part; several Madagascan species]

– Hind tarsomere 1 with wide, dorsal longitudinal groove. . . . . .*Microdon* (*Megodon* Keiser)

45. Compound eye setulose 46

– Compound eye bare 49

46. Thorax with metasternum and anterior anepisternum bare (as in Fig. 115); wing vein M_1 usually processive (apically directed) with respect to vein R_{4+5}, rarely curved basally (Fig. 135). . . . . *Chrysogaster* Meigen [in part]

– Thorax with metasternum and anterior anepisternum setulose (as in Fig. 116); wing vein M_1 recessive with respect to vein R_{4+5}, curved basally (e.g., Figs 141, 149) 47

47. Antennal pedicel greatly elongate, *ca* 1.5 × as long as postpedicel (Figs 28, 46) . . . . *Amphoterus* Bezzi

– Antennal pedicel as long as or shorter than postpedicel (e.g., Fig. 30). 48

48. Head with occiput only slightly expanded (Fig. 29); wing with lower calypter microtrichose, without long setulae (Fig. 181); wing vein M_1 with auxiliary vein at point of medial angulation (Fig. 141) . . . . . .*Eumerus* Meigen [in part]

– Head with occiput greatly expanded, tumid (Fig. 30); wing with long setulae on upper surface of lower calypter (Fig. 180); wing vein M_1 without auxiliary vein at point of medial angulation (Fig. 149) . . . . . .*Megatrigon* Johnson

49. Head with oral margin evenly rounded, not notched anteromedially (Fig. 20); occiput developed dorsally (Fig. 95), with distinct indentation in dorsal ⅓; thorax with complete transverse suture; anepisternum not differentiated into anterior flattened and posterior convex parts . . . . . *Spheginobaccha* de Meijere

– Head with oral margin notched anteromedially (as in Fig. 19); occiput not developed dorsally, without distinct indentation on dorsal ⅓; thorax with incomplete transverse suture; anepisternum differentiated into anterior flattened and posterior convex parts. 50

50. Thorax with anterior anepisternum setulose posterodorsally; scutellum triangular (Fig. 81); all femora with ventroapical spines. . . . . *Myolepta* Newman

– Thorax with anterior anepisternum setulose or bare; scutellum rounded apically (e.g., Fig. 100); fore and mid femora without ventroapical spines 51

51. Thorax with anterior anepisternum setulose posterodorsally (as in Fig. 116) . . . . . .*Eumerus* Meigen [in part]

– Thorax with anterior anepisternum bare (as in Fig. 115) 52

52. Wing vein R_{4+5} virtually straight or strongly sinuate (Fig. 156); crossvein *r–m* positioned at ⅕ of distal end of cell *dm* (Fig. 156); hind femur with 1 large apicoventral spur, apex otherwise unmodified (Fig. 187) . . . . . .*Milesia* Latreille

– Wing vein R_{4+5} virtually straight; crossvein *r–m* positioned at most at ⅓ of distal end of cell *dm* (e.g., Figs 131, 176, 179); hind femur without apicoventral spur, if spur or tooth present, then apex with additional apicoventral carinate expansion (e.g., Figs 192, 193) 53

53. Wing veins R_{4+5} and M_1 gradually converging, meeting just before wing apex (e.g., Figs 131, 177); male with large spur on hind coxa (e.g., Figs 192, 193). 54

– Wing veins R_{4+5} and M_1 not gradually converging, meeting well before wing apex (e.g., Figs 135, 160, 179); male without large spur on hind coxa 55

54. Hind femur with apicolateral expansion notched, forming large spur and carina (Fig. 192); male hind coxa with large spur, male hind trochanter with conspicuous curved expansion (Fig. 192) or long spur (*C. androyensis* Keiser, 1971) (confined to Madagascar) . . . . . *Calcaretropidia* Keiser

– Hind femur with apicolateral expansion notched or unnotched, triangularly produced (Fig. 193); male hind coxa without large spur, male hind trochanter with inconspicuous lamella or unmodified (Central Africa and Madagascar) . . . . . *Tropidia* Meigen

55. Compound eye frequently with pattern (e.g., Fig. 83); hind femur not swollen, without spines (e.g., Fig. 83); wing vein M_1 perpendicular or slightly processive (e.g., Fig. 135) or recessive (e.g., Fig. 160), with respect to vein R_{4+5}; abdomen short, oval 56

– Compound eye without pattern (e.g., Fig. 102); hind femur slightly or strongly swollen, with black apicoventral or apicolateral spines; male femur sometimes with ventral spines (e.g., Fig. 194); wing vein M_1 processive with respect to vein R_{4+5} (e.g., Fig. 179); abdomen elongate, parallel-sided 57

56. Antennal postpedicel at most 1.4 × as long as wide; wing vein M_1 usually processive with respect to wing vein R_{4+5} (apically directed), rarely curved basally (Fig. 135). . . . . *Chrysogaster* Meigen [in part]

– Antennal postpedicel usually at least 2 × as long as wide (Fig. 83); wing vein M_1 recessive with respect to wing vein R_{4+5} (not apically directed), basally curved (Fig. 160) . . . . .*Orthonevra* Macquart [in part]

57. Thorax with subscutellar fringe (as in Fig. 111); metepisternum bare; hind femur not greatly enlarged, with spines, but without anteroventral spinose carina in apical ⅓ (Fig. 194) . . . . . *Xylota* Meigen

– Thorax without subscutellar fringe (with exception of *S. decora* Walker, 1849); metepisternum with patch of fine setulae; hind femur greatly enlarged, with or without spines and with anteroventral spinose carina at apical ⅓ (Figs 97, 195). . . . . .*Syritta* Le Peletier & Serville

58. Wing vein R_{4+5} with auxiliary vein in cell r_{4+5} (e.g., Figs 132, 162); male abdomen with 4 visible abdominal tergites (e.g., Fig. 53) 59

– Wing vein R_{4+5} without auxiliary vein in cell r_{4+5} (e.g., Fig. 161); male abdomen with 5 visible abdominal tergites (e.g., Fig. 206) 60

59. Male antennal postpedicel with long setulae (Figs 24, 53); abdominal tergites 3 and 4 unfused, able to articulate independently . . . . . *Ceratrichomyia* Séguy [in part; *C. angolensis* Reemer, 2013]

– Male antennal postpedicel without long setulae (Fig. 85); abdominal tergites 3 and 4 fused, unable to articulate independently . . . . . .*Paramixogaster* Brunetti

60. Abdominal tergite 1 well-developed, especially on disc, where frequently ½ as long as tergite 2, invariably extending well beyond scutellum (Fig. 206), sublaterally *ca* ¾ as long as tergite 2; tergites minutely punctate (Fig. 206). . . . . *Paragus* Latreille 61

– Abdominal tergite 1 greatly reduced, frequently almost linear on disc, virtually obscured by scutellum, sublaterally at most ½ as long as tergite 2 (e.g., Fig. 199); tergites not punctate. 64

61. Compound eye uniformly setulose, of virtually uniform colour, not forming vittae of contrasting colour (Fig. 33); thorax with scutellum entirely black . . . . . .*Paragus* (*Pandasyopthalmus* Stuckenberg)

– Compound eye with ommatrichia arranged in alternate, more or less vertical vittae, of different colours or reflecting light differently (e.g., Figs 34, 35); thorax with scutellum entirely black or black with apex narrowly yellow or reddish (e.g., Fig. 108) 62

62. Compound eye (in dorsolateral view), with 2 dark and 3 more distinct white dorsoventral fascia of ommatrichia (vittae) (Fig. 35); scutellum with conspicuous short, thick spines on posterior margin (at least 2 × as long as wide) (Fig. 108). . . . . *Paragus* (*Serratoparagus* Vujić & Radenković)

– Compound eye (in dorsolateral view), with 2 (or 3) white dorsoventral fascia of ommatrichia (vittae) among dark ommatrichia (e.g., Figs 34, 84); scutellum with posterior margin without conspicuous teeth (smooth or < 2 × as long as wide) (e.g., Fig. 206) 63

63. Abdominal tergites 1–5 entirely fused, at least laterally (Figs 84, 206); male terminalia with epandrium at narrowest part ½–⅔ length of cercus . . . . . *Paragus* (*Afroparagus* Vujić & Radenković)

– Abdomen tergites 1–2 entirely fused; male terminalia with epandrium at narrowest part 2 × length as cercus . . . . . *Paragus sensu stricto*

64. Abdomen elongate, petiolate, with tergite 2 narrower than tergite 3 (e.g., Figs 2, 44, 89) 65

– Abdomen parallel-sided to oval, never distinctly petiolate (e.g., Figs 3, 4, 9). 66

65. Thorax with katatergite setulose, at least with patch of long setulae dorsally; postpronotum and/or anterior anepisternum setulose; metepisternum setulose; scutum usually with well-developed collar of longer setulae at anterior margin . . . . . .*Allobaccha* Curran

– Thorax with katatergite, anterior anepisternum and metepisternum bare; scutum without setulae collar at anterior margin . . . . . *Pseudodoros* Becker

66. Head with face entirely black in ground colour (e.g., Figs 42, 73), but strongly yellow setulose and pruinescent in *Xanthandrus* Verrall (e.g., Fig. 101); compound eye bare; thorax with metasternum bare; scutellum entirely black in ground colour; abdomen usually without marginal groove (e.g., Fig. 205) 67

– Head with face at least partly yellow or yellowish brown in ground colour (e.g., Figs 45, 50, 57, 66, 68); compound eye bare or setulose; scutellum often yellowish brown or partly yellow; thorax with metasternum setulose or bare; in doubtful cases (e.g., Fig. 51) eyes pilose; abdomen usually with marginal groove. 70

67. Thorax with metepisternum with some fine, subappressed setulae; katepisternum with setulae patches broadly separated posteriorly, joined anteriorly (Fig. 114); hind coxa with tuft of setulae at posteromedial apical angle . . . . . .*Xanthandrus* Verrall

– Thorax with metepisternum bare; katepisternum with setulae patches broadly separated throughout; hind coxa with or without tuft of setulae 68

68. Legs with hind coxa with tuft of setulae at posteromedial apical angle; hind femur swollen, about 2 × as broad as hind tibia (Fig. 86); thorax with metasternum entire, well-developed . . . .*Pelloloma* Vockeroth

– Legs with hind coxa without posteromedial apical setulae tuft; hind femur simple, not swollen, about as broad as hind tibia (e.g., Figs 42, 73); thorax with metasternum entire or reduced 69

69. Thorax with metasternum entire (as in Fig. 118). . . . . .*Afrostoma* Skevington, Thompson & Vockeroth

– Thorax with metasternum greatly reduced, with deep posterior incision laterally, so sclerotised part consists of median diamond-shaped area, with narrow anterior and lateral fascia (Fig. 119) . . . . . *Melanostoma* Schiner

70. Wing vein R_{4+5} sinuate, looped into cell r_{4+5} (Fig. 136); compound eye densely long pilose; antennae almost as long as head (Figs 43, 56) . . . . . *Chrysotoxum* Meigen

– Wing vein R_{4+5} not sinuate, not looped into cell r_{4+5} (e.g., Fig. 123); compound eye bare to densely pilose; antennae almost as long as head or much shorter than head. 71

71. Compound eye pilose 72

– Compound eye bare 74

72. Compound eye sparsely and short pilose; hind femur and tibia with brushes of long setulae (Fig. 43); hind coxa without tuft of strong setulae at posteromedial apical angle; antennal scape *ca* 3 × as long as pedicel (Fig. 43). . . . . *Afrosyrphus* Curran

– Compound eye densely pilose (Fig. 51); hind femur and tibia without brushes of long setulae (Fig. 43); antennal scape at most 2 × as long as pedicel (only in *Betasyrphus inflaticornis* (Bezzi, 1915) *ca* 3 × as long as pedicel) 73

73. Wing membrane microtrichia well-developed, at least apical ⅓ densely and uniformly microtrichose; wing vein R_{4+5} virtually straight; lower lobe of calypter setulose, especially on posteromedial part (Fig. 182), pilosity sometimes reduced to only a few long setulae; thorax without yellow lateral vitta on scutum (widespread Afrotropical Region) . . . . . *Betasyrphus* Matsumura

– Wing membrane sparsely microtrichose, with extensive bare areas also on apical ⅓; wing vein R_{4+5} distinctly angled; lower lobe of calypter bare; thorax with ill-defined yellow lateral vitta on scutum (Cabo Verde and Mediterranean province) . . . . . *Scaeva* F.

74. Compound eye with distinct triangular emargination at posterior margin, at or dorsal to level of antennal insertion (Figs 38, 99) . . . . . *Toxomerus* Macquart

– Compound eye without distinct triangular emargination at posterior margin (e.g., Figs 45, 57) 75

75. Thorax with anterior anepisternum setulose, at least posterodorsally (as in Fig. 116); wing margin with series of minute closely spaced black maculae on posterior margin 76

– Thorax with anterior anepisternum bare (as in Fig. 115); wing margin without series of minute closely spaced black maculae 77

76. Thorax with metasternum setulose; metepisternum setulose ventral to spiracle . . . *Episyrphus* Matsumura

– Thorax with metasternum and metepisternum bare . . . . . *Meliscaeva* Frey

77. Abdomen without marginal groove (e.g., Fig. 205) 78

– Abdomen with at least weak marginal groove on tergites 4–5, often with strong groove on tergites 3–5 (e.g., Fig. 204) 81

78. Thorax with yellow lateral vitta on scutum not extending beyond transverse suture (e.g., Figs 66, 94) . . . . . *Sphaerophoria* Le Peletier & Serville [in part] 79

– Thorax with yellow lateral vitta on scutum extending from postpronotum to scutellum (e.g., Figs 3, 45) 80

79. Head with broad black facial vitta (Fig. 66); thorax with subscutellar fringe well-developed (as in Fig. 111), except on medial ⅓; male terminalia small, with tergite 9 at most ½ as wide as abdomen; female tergite 5 with distinct yellow maculae isolated from lateral margins . . . . . *Sphaerophoria* (*Exallandra* Vockeroth)

– Head with face yellow (Fig. 94); thorax without subscutellar fringe; male terminalia large, globose, with tergite 9 as wide as abdomen; female tergite 5 either without yellow maculae or yellow maculae broadly reaching lateral margin . . . . . *Sphaerophoria* (*Loveridgeana* Doesburg & Doesburg) [in part]

80. Male eyes holoptic; female face without carina; thorax with subscutellar fringe complete, dense (as in Fig. 111); male terminalia small, inconspicuous (Fig. 45), with tergite 9 at most ½ as wide as abdomen (widespread continental Afrotropics; not Saint Helena Is.) . . . . . *Allograpta* Osten Sacken

– Male eyes dichoptic; female face with distinct median carina, extending from antenna to callus; thorax without subscutellar fringe; male terminalia large, globose, with tergite 9 as wide as abdomen (confined to Saint Helena Is.; *S.* (*Loveridgeana*) *beattei* (Doesburg & Doesburg, 1976)) . . . . . *Sphaerophoria* Le Peletier & Serville [in part]

81. Head with face markedly produced forward (Fig. 50); thorax with metapleuron with tuft of fine setulae ventral to spiracle; metasternum setulose; large species (length: 8–14 mm), with broad flattened abdomen (Figs 4, 50), with distinct marginal groove (Fig. 204) . . . . . *Asarkina* Macquart 82

– Head with face not markedly produced forward (e.g., Figs 65, 68); thorax with metapleuron bare ventral to spiracle; metasternum bare or setulose; small to large species (length: < 15 mm), with slender to oval abdomen (e.g., Fig. 68), without distinct marginal groove 83

82. Thorax without collar of setulae on mesonotum; wing vein R_{4+5} virtually straight . . . . . *Asarkina* (*Achoanus* Munro)

– Thorax with distinct collar of longer, denser setulae on anterior part of mesonotum; wing vein R_{4+5} moderately sinuate (Fig. 129) . . . . . *Asarkina sensu stricto*

83. Scutum dark laterally, without vitta (Figs 9, 65); thorax with metasternum setulose; wing membrane (Fig. 142) densely microtrichose in apical ⅓; male hind coxa without ventral spine . . . . . *Eupeodes* Osten Sacken

– Scutum with bright yellow vitta, extending from postpronotum to halfway between scuttelar suture to scutellum (Fig. 68); thorax with metasternum bare; wing membrane with sparse, scattered microtrichia in apical ⅓ (Fig. 145); male hind coxa with (Fig. 197) or without ventral spine . . . . . *Ischiodon* Sack

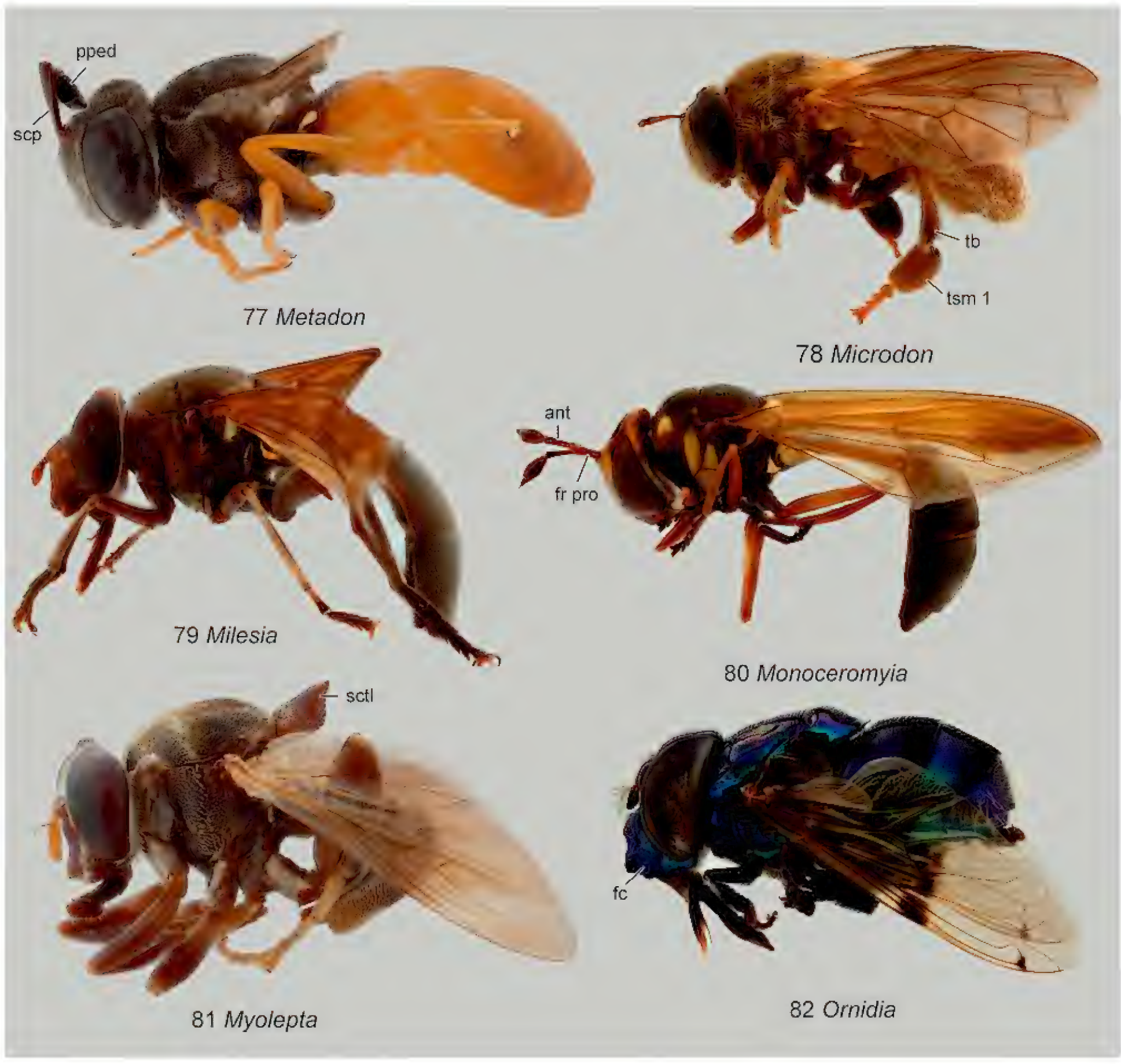
Figs 60.71–76. Habitus of Syrphidae (lateral views): (71) *Mallota* sp.; (72) *Megatrigon* sp.; (73) *Melanostoma* sp.; (74) *Merodon* sp.; (75) *Meromacroides meromacriformis* (Bezzi); (76) *Mesembrius* (*Mesembrius*) sp.

Abbreviations: fc – face; cal – callus; fem – femur; pprn – postpronotum.

Synopsis of the fauna

Afromicrodon **Thompson** (Microdontinae: Microdontini)**.** An endemic genus of five species confined to Comoros and Madagascar. *Afromicrodon* are small-sized (length: 6–9 mm) flies, with a short antenna and an oval abdomen (Figs 1, 41). Together with *Spheginobaccha*, these are the only Afrotropical Microdontinae that lack a posterior auxiliary vein on wing vein R_{4+5} in cell r_{4+5} (Fig. 121). Afrotropical species of the genus were previously placed in the genus *Ceratophya* Wiedemann, but this is restricted to the Neotropical Region. Biology and immature stages remain unknown, but larvae probably occur with ants and in their nests, as do other Microdontinae. No identification key to Afrotropical species is currently available.

Afrostoma **Skevington, Thompson & Vockeroth** (Syrphinae: Syrphini)**.** An endemic, monotypic genus, with the single described species, *A. quadripunctatum* Skevington, Thompson



Figs 60.77–82. Habitus of Syrphidae (lateral views): (77) *Metadon* sp. (wings missing); (78) *Microdon tarsalis* Hervé-Bazin.; (79) *Milesia* sp.; (80) *Monoceromyia* sp.; (81) *Myolepta* sp.; (82) *Ornidia obesa* (F.).

Abbreviations: ant – antenna; scp - scape; fc – face; fr pro – frontal prominence; pped – postpedicel; sctl – scutellum; tb – tibia; tsm – tarsomere.

& Vockeroth, 2014 (Fig. 42), described from East Africa (Kenya and Uganda) and several undescribed species. *Afrostoma quadripunctatum* is a slender, small-sized (length: 7–8 mm) species that is morphologically close to *Melanostoma* (Fig. 73), but differs from it in the entire metasternum and straighter face with a stronger callus (Fig. 42). Recently, Mengual (2019) synonymised both genera. Presumably, larvae are predatory on Sternorrhyncha (Hemiptera), but biology and immature stages remain unknown.

***Afrosyrphus* Curran** (Syrphinae: Syrphini)**.** An endemic genus of two species, *A. varipes* Curran, 1927 (Fig. 43), described from

Figs 60.83–88. Habitus of Syrphidae (lateral views): (83) *Orthonevra* sp.; (84) *Paragus* (*Afroparagus*) sp.; (85) *Paramixogaster* sp.; (86) *Pelloloma nigrifacies* Vockeroth; (87) *Phytomia natalensis* (Macquart); (88) *Polybiomyia* sp.

Abbreviations: fem – femur; pped – postpedicel.

the Democratic Republic of Congo, but also occurring in Angola, Cameroon, Kenya and South Africa and *Afrosyrphus schmuttereri* Mengual, Ssymank, Skevington, Reemer & Ståhls, 2020 from Kenya and Uganda (Mengual *et al*. 2020). *Afrosyrphus* are medium-sized (length: 9–10 mm) mimics of stingless bees and have setulose hind legs and a long, upwardly directed antenna, with the postpedicel 4–5 × as long as wide (Fig. 43). Species of the genus occur in forests but are scarce and are known to visit flowers of *Phyllanthus discoideus* Müll.Arg. (Euphorbiaceae) (A. Ssymank, unpubl.). Schmutterer (1974) found abundant larvae of *A. varipes* feeding on different species of aphids (Hemiptera: Sternorrhyncha: Aphidoidea), the larvae concerned

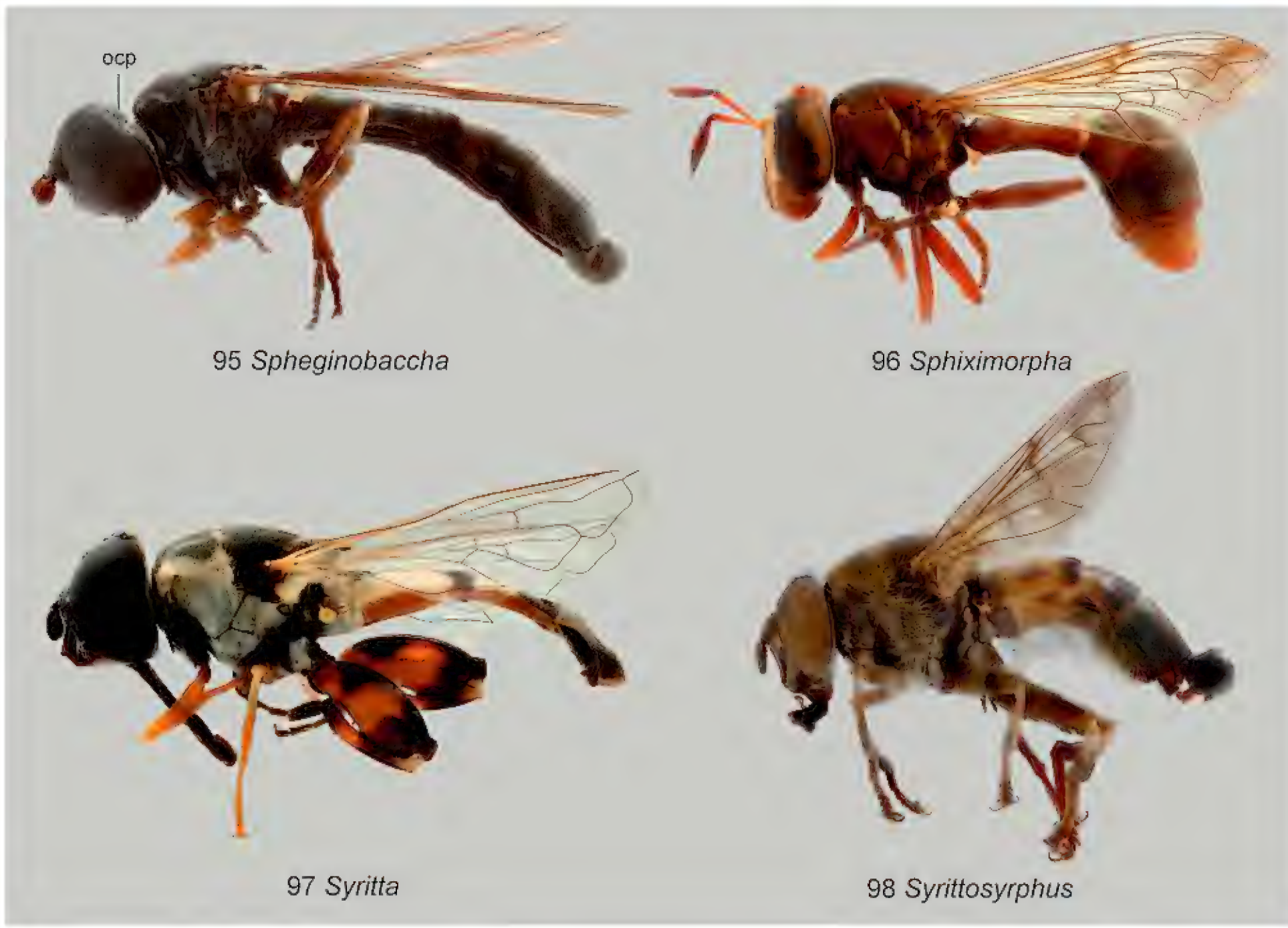
Figs 60.89–94. Habitus of Syrphidae (lateral views): (89) *Pseudodoros nigricollis* Becker; (90) *Ptilobactrum neavei* Bezzi; (91) *Rhingia* (*Rhingia*) sp.; (92) *Senaspis dentipes* (Macquart); (93) *Simoides crassipes* (F.); (94) *Sphaerophoria* sp.

Abbreviations: fc – face; sct – scutum.

representing an undescribed species (Mengual *et al*. 2020). The biology and immature stages otherwise remain unknown.

***Allobaccha* Curran** (Syrphinae: Syrphini)**.** An Old World genus of *ca* 88 species, recorded from the Afrotropical and Palaearctic Regions. Thirty-two species occur in the Afrotropics, plus several undescribed species (X. Mengual, pers. comm. 2019), distributed over the entire region. Species of this genus were formerly placed in the genus *Baccha* Meigen, but that genus is restricted to the Holarctic Realm. *Allobaccha* are small- to large-sized (length: 5–19 mm) flies, with a long, slender and petiolate abdomen (Figs 2, 44). Numerous species have infuscate, maculate and/or fasciate wings (Figs 44, 124). They occur in a wide range of habitats types, from savanna, wetlands, scrub, open patches and shaded areas in forests with a well-developed shrub layer and in urban areas. The *A. "picta* species-group" with dark wings (Fig. 44) occurs in subtropical forests, riverine tropical forests and cocoa plantations. Larvae occur on plants in shaded areas and feed on Aphididae (Hemiptera). Adults have been recorded on flowering trees, such as "*Acacia*" (Fabaceae), *Berlinia grandiflora* (Vahl) Hutch. & Dalziel (Fabaceae) and *Phyllanthus* (Euphorbiaceae) and on flowers of different herbs, such as *Alepidia* (Apiaceae) and *Plectranthus* (Lamiaceae) (Classen *et al*. 2020). Identification keys to Afrotropical species were provided by Curran (1938*b*) (as *Baccha*, for 21 species) and Dirickx (2010) for Malagasy species.

***Allograpta* Osten Sacken** (Syrphinae: Syrphini)**.** A virtually cosmopolitan genus, in both the broad (Mengual *et al*. 2009) and restricted sense (Thompson 2012). In the restricted sense, it comprises 68 species globally, 12 of which occur in the Afrotropical Region, widely distributed in the entire region. *Allograpta* are small- to medium-sized (length: 6.6–10 mm), slender flies, with a bright yellow lateral vitta on the scutum and a black and yellow abdomen (Figs 3, 45). Larvae are predators of Aphididae and adults have been recorded on flowers of a wide variety of tree, shrub and herb species, e.g., *Begonia* (Begoniaceae), *Dipsacus pinnatifidus* Steud. ex A.Rich. (Dipsacaceae) and *Gnaphalium fruticosum* Forssk. (Asteraceae) (Classen *et al*. 2020). The biology otherwise remains poorly documented. An identification key to seven Afrotropical species was provided by Curran (1938*b*) (as *Syrphus*).



Figs 60.95–98. Habitus of Syrphidae (lateral views): (95) *Spheginobaccha* sp.; (96) *Sphiximorpha* sp.; (97) *Syritta flaviventris* Macquart; (98) *Syrittosyrphus opacea* Hull.

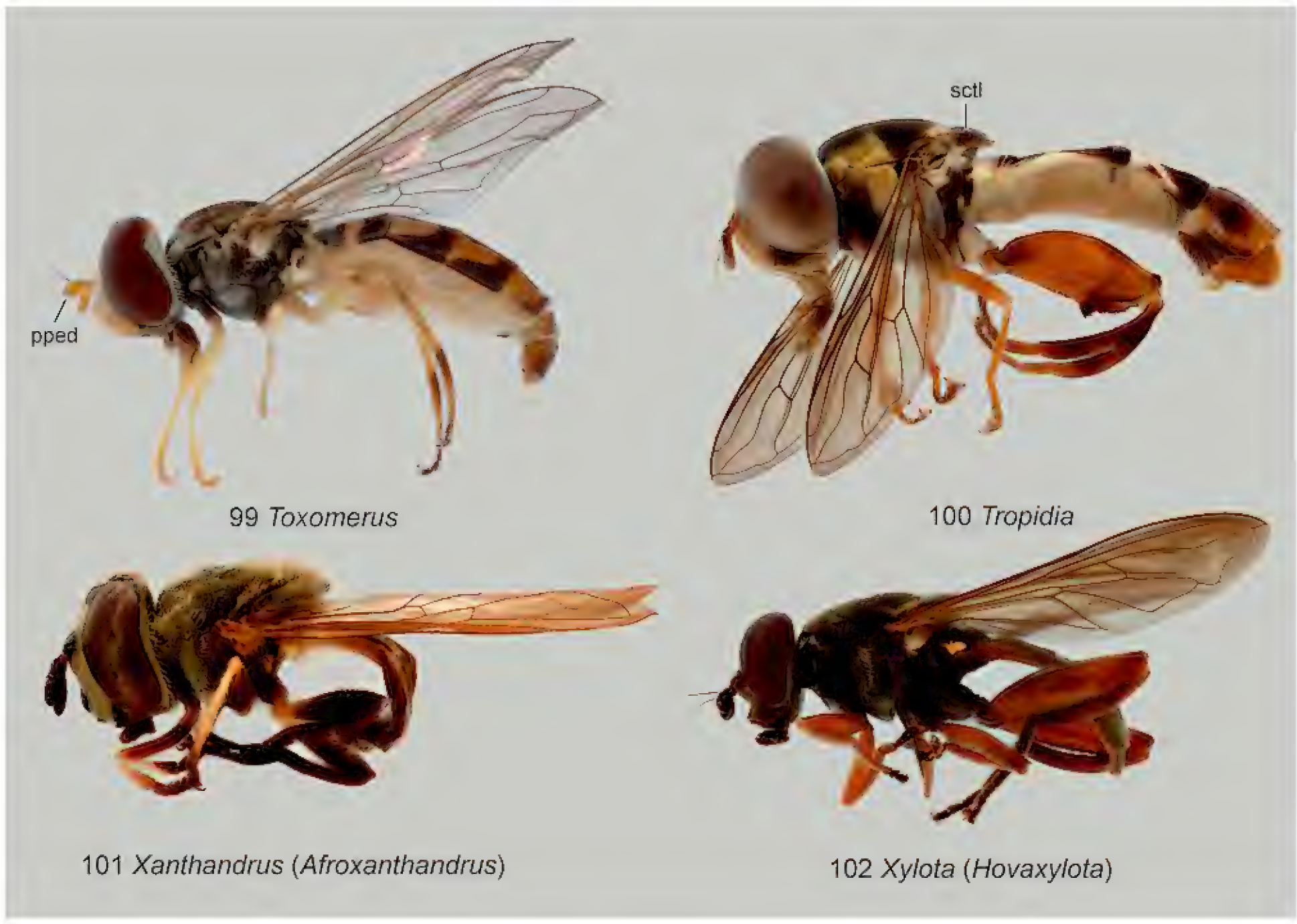
Abbreviation: ocp – occiput.

***Amphoterus* Bezzi** (Eristalinae: Eumerini)**.** An endemic genus with two described species, *A. braunsi* Doesburg, 1956 (Fig. 46) described from South Africa and *A. cribratus* Bezzi, 1915, described from Kenya. *Amphoterus* are medium-sized (length: 9–11 mm) flies, resembling *Eumerus* in wing venation, but with a greatly elongated antennal pedicel, which is distinctly longer than the postpedicel (Figs 28, 46). Biology and immature stages remain unknown. An identification key is unavailable.

***Anasimyia* Schiner** (Eristalinae: Eristalini)**.** A genus of *ca* 13 species occurring in the Afrotropical, Nearctic and Palaearctic Regions. Three species occur in the Afrotropics: *A. katonae* (Bezzi, 1921) described from Tanzania; *A. nasutus* (Curran, 1929) described from Democratic Republic of Congo; and *A. rhinosus* (Hull, 1944) described from Uganda. *Anasimyia* are small- to medium-sized (length: 8–10 mm) flies with a conically produced face (Fig. 47) and a strongly sinuate wing vein R_{4+5} (Fig. 127). Larvae of Palaearctic species have been found slightly below the water surface, between decaying leaf sheaths of *Typha latifolia* L. (Typhaceae) (Harteley 1961). Adults occur in the vicinity of water with rich marginal vegetation. An identification key to two Afrotropical species (as *Lejops*) was provided by Curran (1939*a*). The *Anasimyia* species in the Afrotropics almost certainly should be attributed to a new genus based on unpublished molecular phylogenetic and morphological work (Moran *et al.*, unpubl.).

***Archimicrodon* Hull** (Microdontinae: Microdontini)**.** A mainly Old World genus of 44 described species, occurring in the Afrotropical, Australasian, Oriental and Palaearctic Regions. There are 21 described species recorded from the Afrotropics, six of which belong to the endemic Malagasy subgenus *A.* (*Hovamicrodon* Keiser), which has spoon-shaped scutellar processes (Fig. 110). *Archimicrodon* are small- to medium-sized (length: 5–12 mm) flies (Figs 48, 49). Larvae of an Australian species have been found in an unidentified ants' nest and it is likely that all species of this genus develop in ants' nests. Biology and immature stages are otherwise unknown. The identification key of Curran (1938*a*) to Afrotropical species of "*Microdon*" includes eight species currently included in *Archimicrodon*.

***Asarkina* Macquart** (Syrphinae: Syrphini)**.** An Old World genus of *ca* 49 species, with its main distribution in the



Figs 60.99–102. Habitus of Syrphidae (lateral views): (99) *Toxomerus floralis* (F.); (100) *Tropidia* sp.; (101) *Xanthandrus* (*Afroxanthandrus*) sp.; (102) *Xylota* (*Hovaxylota*) sp.

Abbreviations: pped – postpedicel; sctl – scutellum.

Afrotropical and Oriental Regions, with one species in southern Europe and another extending into the Far Eastern Palaearctic (Russia and Japan). Twenty-one species are recorded from the Afrotropics that are widely distributed throughout the region. One species, *A. hulleyi* Munro, 1924, described from South Africa, is placed in the separate endemic subgenus *A.* (*Achoanus* Munro). *Asarkina* are small- to medium-sized (length: 8–14 mm), brightly orange and black coloured flies, with a broad oval abdomen and bare eyes (Figs 4, 50). They mainly inhabit tropical forests, cloud forests and shrubland, with a higher species diversity in mountainous areas. Larvae are important predators of Aphididae, but biology and ecology of many species remain poorly documented. Adults are important pollinators, observed on trees, such as Mango, *Mangifera indica* L. (Anacardiaceae) and *Ilex mitis* (L.) Radlk. (Aquifoliaceae), as well as on herbs, such as *Ageratum conyzoides* L. (Asteraceae) and *Plectranthus* (Lamiaceae) (A. Ssymank, unpubl.). An identification key to 15 Afrotropical species was provided by Curran (1938*b*).

***Betasyrphus* Matsumura** (Syrphinae: Syrphini)**.** A genus with 19 species occurring in the Afrotropical, Oriental and Palaearctic Regions. The 12 Afrotropical species are widely distributed in the region. *Betasyrphus* are medium-sized (length: 9–12 mm) flies, with a broad abdomen, usually dark coloured, with grey, yellow or orange maculae or fasciae (Figs 5, 51) and are easily distinguished from other Afrotropical Syrphinae by the setulose lower lobe of the calypter (Fig. 182). The genus mostly inhabits various forest types and shrublands, from the lowlands to higher elevations on mountains. Larvae are Aphididae predators, but the biology is poorly documented. Adults are pollinators on a wide range of mostly herbaceous plants, such as the botanical families Apiaceae, Asteraceae (e.g., *Ageratum conyzoides*, *Euryops* and *Senecio*), Dipsacaceae, Euphorbiacae, Rubiaceae and Scrophulariaceae (A. Ssymank, unpubl.). An identification key to Afrotropical species was provided by Curran (1938*b*) (as *Syrphus* "Section 1", including eight species) and Ssymank (2010) provided an identification key to Malagasy species. A revision of the genus is currently in preparation by Ssymank *et al*. (unpubl.).

103 *Mesembrius* (*Mesembrius*)

104 *Asarkina* (*Asarkina*)

105 *Syrittosyrphus*

106 *Eristalinus* (*Eristalinus*)

107 *Eristalis* (*Eoseristalis*)

Figs 60.103–107. Thoraces and scutellum of Syrphidae (lateral views): (103) thorax of *Mesembrius* (*Mesembrius*) sp., lateral view; (104) same, *Asarkina* (*Asarkina*) sp.; (105) scutellum of *Syrittosyrphus opacea* Hull, lateral view; (106) thorax of *Eristalinus* (*Eristalinus*) sp., lateral view; (107) same, *Eristalis* (*Eoseristalis*) sp.

Abbreviations: anepm – anepimeron; ap m – apical margin; pprn – postpronotum; p spr – posterior spiracle; sctl – scutellum.

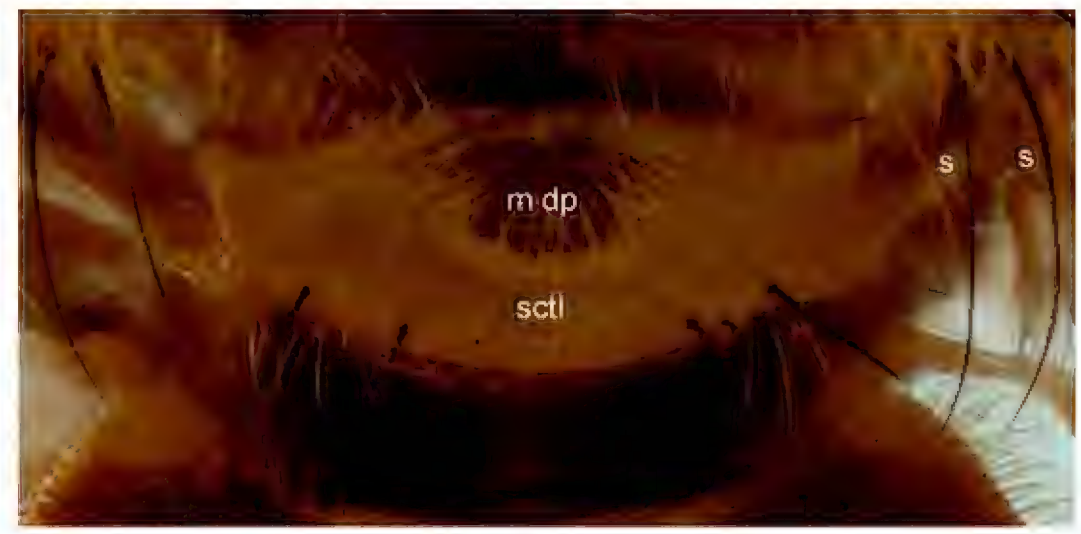
***Calcaretropidia* Keiser** (Eristalinae: Milesiini)**.** An endemic genus of four species confined to Madagascar. *Calcaretropidia* (Fig. 52) are medium-sized (length: 9–13 mm), bright yellow to orange and black coloured flies, with a swollen hind femur bearing an apicoventral notched expansion with a large spur (Fig. 192). Biology and immature stages remain unknown. No identification key is currently available.

Ceratrichomyia Séguy (Microdontinae: Microdontini)**.** An endemic genus of three described species. Two species, *C. behara* and *C. bullabucca*, are endemic to Madagascar and *C. angolensis*, was described from Angola. *Ceratrichomyia* (Fig. 53) are small- to medium-sized (length: 7–10 mm), slender flies, with a complete transverse suture to the thorax, a constricted abdomen and, in the male, a postpedicel with long pilosity (Fig. 24). The biology remains unknown, but larvae probably occur in ants' nests, as is the case with other Microdontinae. No identification key is currently available, but Reemer & Ståhls (2013*a*) provide diagnoses and figures.

***Ceriana* Rafinesque** (Eristalinae: Cerioidini)**.** A north temperate, predominantly Old World genus, with 66 described species, occurring in the Afrotropical and Neotropical Regions. Five species are recorded from the Afrotropics, distributed in Burkina Faso, Democratic Republic of Congo, Namibia and Zimbabwe. *Ceriana* (Fig. 54) are medium- to large-sized (length: 12–15 mm), slender wasp-mimics without a constricted second abdominal segment, with long, proerect antennae on a long frontal prominence, which is at least as long as the antennal pedicel (Fig. 54) and with wing crossvein *r–m* inserted at, or beyond the middle of wing cell *dm* and a moderately sinuose wing vein R_{4+5} (Fig. 133). Larvae occur in sap runs of deciduous trees (Rotheray *et al*. 1998) and are saprophagous, mostly in decaying plant sap. Adults visit flowers of *Phyllanthus discoideus* (Euphorbiaceae) and possibly other trees and lianas (A. Ssymank, pers. obs.). An identification key to Afrotropical species was provided by Thompson (2013).

***Chasmomma* Bezzi** (Eristalinae: Eristalini)**.** An endemic genus of five species, distributed in the entire Afrotropical Region, except Southern Africa. *Chasmomma* (Fig. 55) are small- to medium-sized (length: 7–12 mm), blackish flies, with a swollen hind femur and bare eyes, these being dichoptic in males (Fig. 14). Adults rest on vegetation near small streams in forests. Biology and immature stages otherwise remain unknown. An identification key was provided by Kassebeer (2000*a*).

108 *Paragus* (*Serratoparagus*)



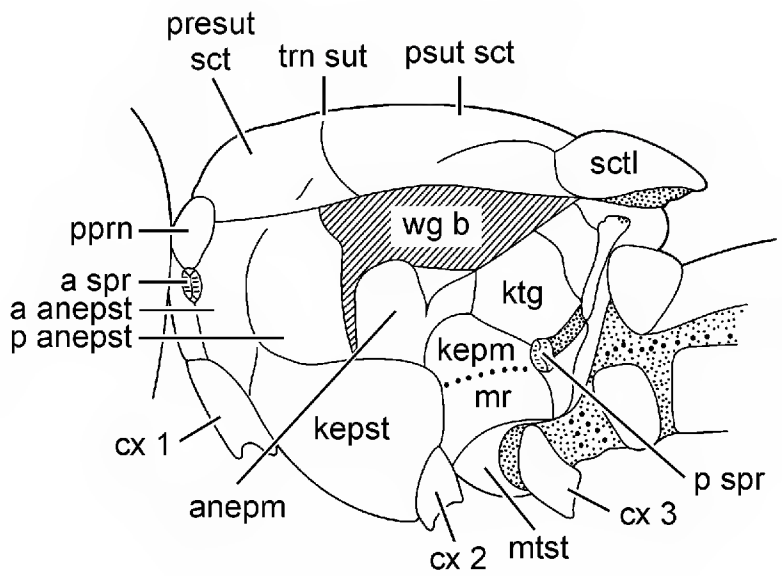
109 *Graptomyza*

110 *Archimicrodon* (*Hovamicrodon*)

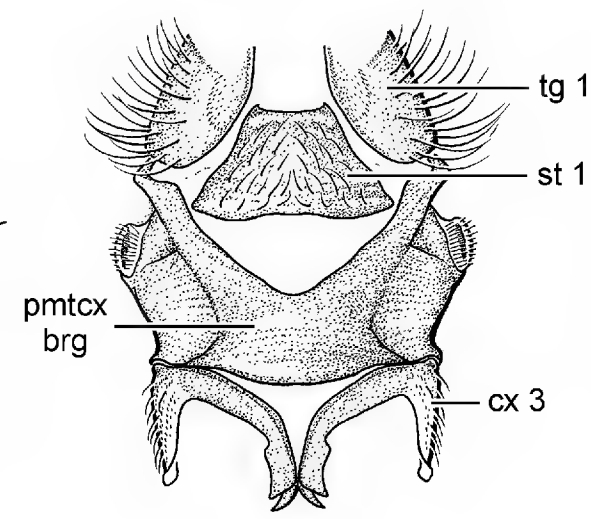
111 *Asarkina* (*Asarkina*)

Figs 60.108–111. Scutella of Syrphidae (dorsal views): (108) *Paragus* (*Serratoparagus*) sp., dorsal view; (109) *Graptomyza* sp.; (110) *Archimicrodon* (*Hovamicrodon*) sp.; (111) *Asarkina* (*Asarkina*) sp.

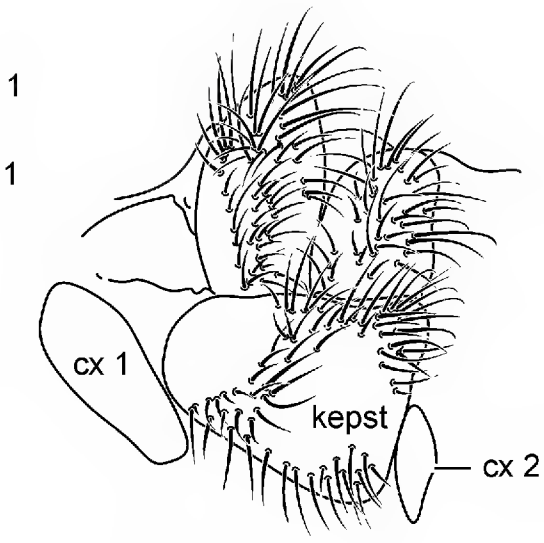
Abbreviations: m dp – median depression; s – seta; sbsctl fr – subscutellar fringe; sctl – scutellum.



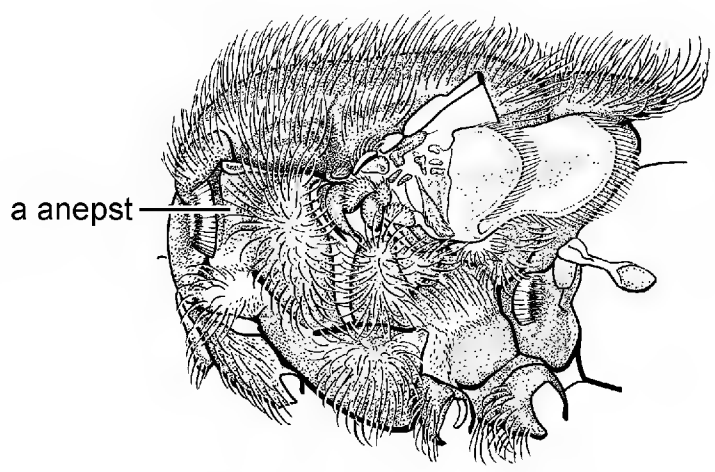
112 Syrphidae



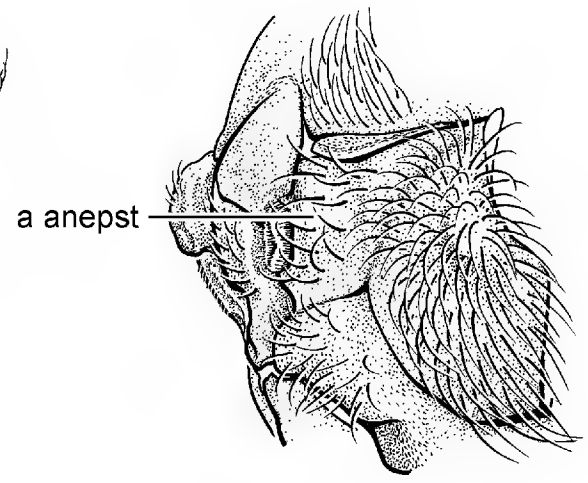
113 *Polybiomyia*



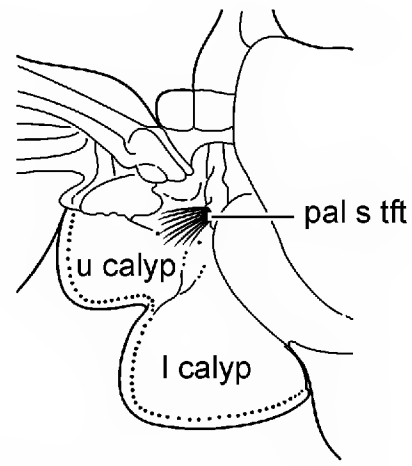
114 *Xanthandrus* (*Afroxanthandrus*)



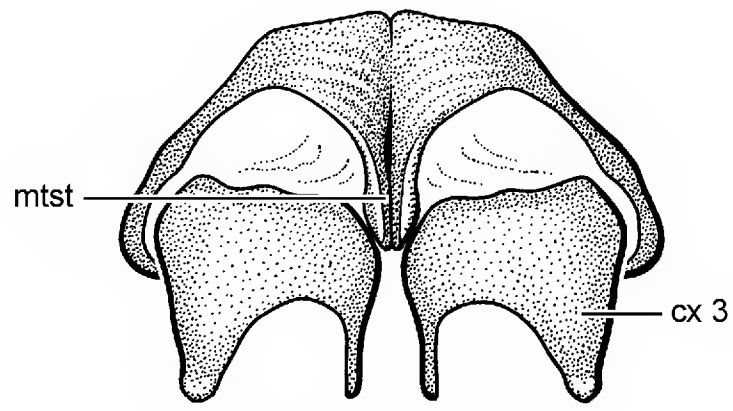
115 *Eristalinus* (*Eristalinus*)



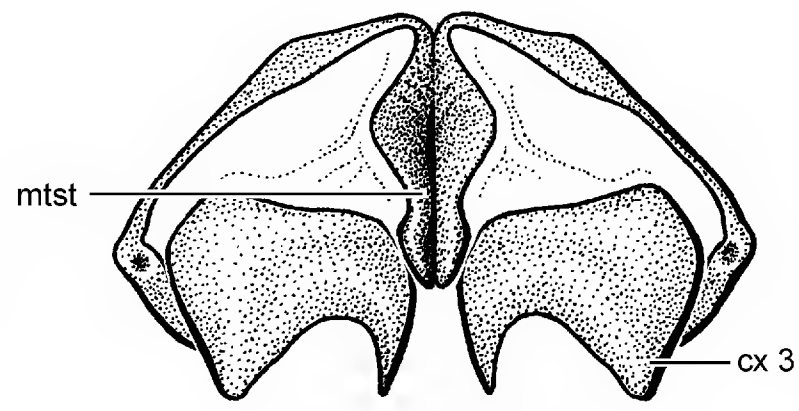
116 *Meliscaeva*



117 *Pseuderistalis*



118 *Platycheirus*



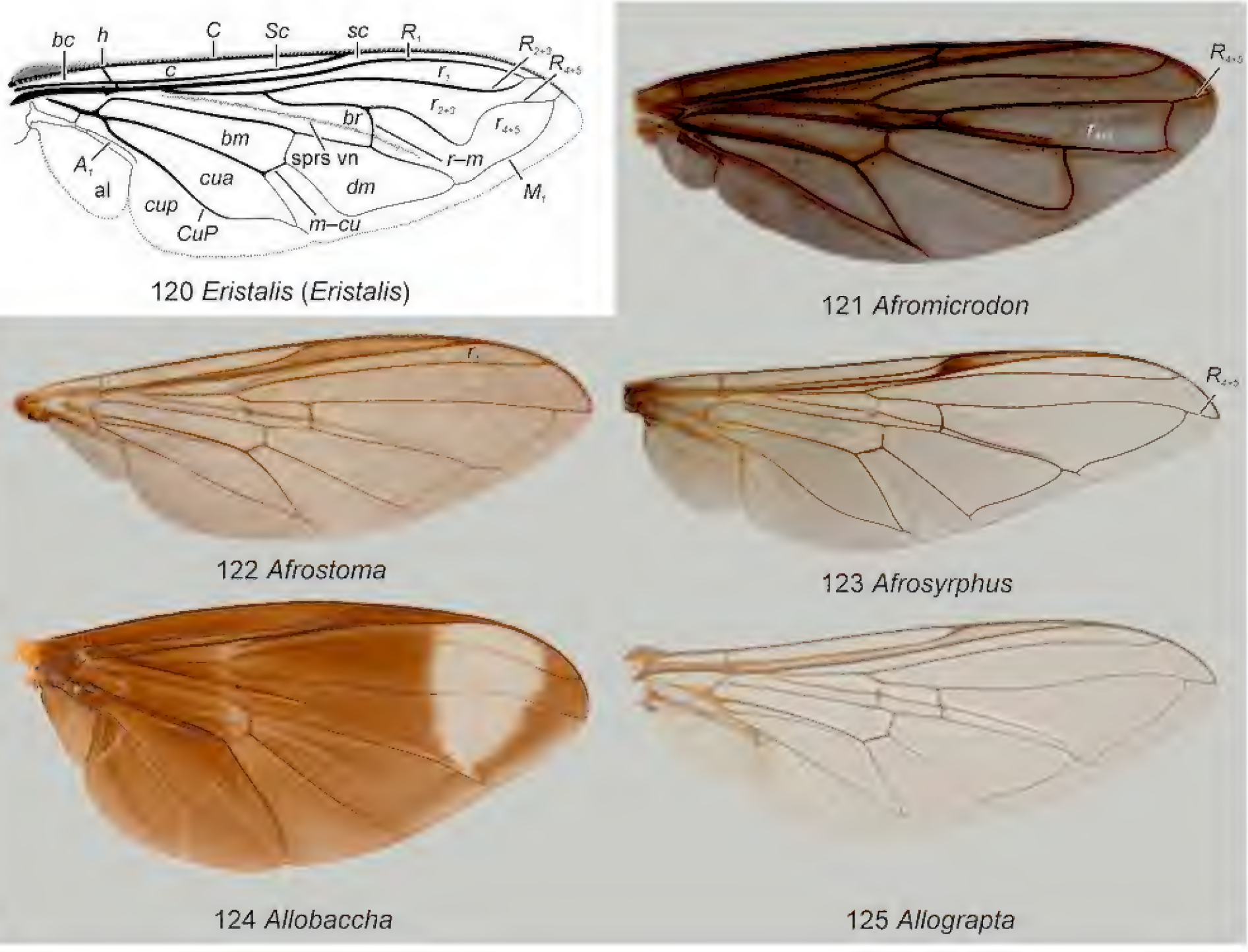
119 *Melanostoma*

Figs 60.112–119. Thoraces of Syrphidae: (112) diagrammatic representation of Syrphidae, lateral view; (113) *Polybiomyia townsendi* (Snow), ventral view (non-Afrotropical); (114) *Xanthandrus* (*Afroxanthandrus*) sp., lateral view; (115) same, *Eristalinus* (*Eristalinus*) *aeneus* (Scopoli) (non-Afrotropical); (116) same, *Meliscaeva cinctella* (Zetterstedt) (non-Afrotropical); (117) *Pseuderistalis viridis* (Coquillett), dorsal view (non-Afrotropical); (118) *Platycheirus quadratus* (Say), ventral view (non-Afrotropical); (119) same, *Melanostoma mellinum* (L.) (non-Afrotropical). Fig. 112 (after Thompson, 1999, fig. 8), Figs 113–116, 118, 119 (after Vockeroth & Thompson 1987, figs 64, 65, 70, 71, 81), Fig. 117 (after Thompson & Rotheray 1998, fig. 74).

Abbreviations: a anepst – anterior anepisternum; a spr – anterior spiracle; anepm – anepimeron; cx – coxa; kepm – katepimeron; kepst – katepisternum; ktg – katatergite; l calyp – lower calypter; mr – meron; mtst – metasternum; p anepst – posterior anepisternum; p spr – posterior spiracle; pal s tft – postalar setal tuft; pmtcx brg – postmetacoxal bridge; pprn – postpronotum; presut sct – presutural scutum; psut sct – postsutural scutum; sctl – scutellum; st – sternite; tg – tergite; trn sut – transverse suture; u calyp – upper calypter; wg b – wing base.

***Chrysogaster* Meigen** (Eristalinae: Brachyopini)**.** A genus of *ca* 40 species occurring mostly in the Afrotropical and Palaearctic Regions. There are ten Afrotropical species described as *Chrysogaster*, but some probably belong in the genus *Orthonevra* and molecular phylogenetic work suggests that both genera have to be redefined in the Afrotropical Region (Moran *et al*., unpubl.). They are widely distributed in the continental Afrotropics, with one species known from Madagascar. *Chrysogaster* are small-sized (length: 4–7 mm), blackish to metallic flies, with a very characteristic wing venation (Fig. 135). Larvae are aquatic detritus-feeders, occurring in the mud along river margins and in marshes. An identification key to three Afrotropical species was provided by Bezzi (1915: 15).

***Chrysotoxum* Meigen** (Syrphinae: Syrphini)**.** A north temperate genus of more than 100 species, occurring in the Afrotropical, Neotropical, Oriental and Palaearctic Regions. The single Afrotropical species, *C. continum* Bezzi, 1915, was described from Kenya and is distributed in East and Central Africa and in Yemen (Smit *et al*. 2017). *Chrysotoxum* (Figs 6, 56) are medium- to large-sized (length: 8–17 mm) wasp-mimics, with long proerect antennae and a yellow and black, broadly oval abdomen. They occur at forest margins, in open mountain shrublands and heathland and in tall herb and fern vegetation. Flower visits have been observed on Asteraceae, including *Ageratum conyzoides*, *Emilia discifolia* (Oliv.) C. Jeffrey, *Euryops chrysanthemoides* (DC.) B. Nord. and *Helichrysum forskalii* (Classen *et al*. 2020). Larvae of extralimital



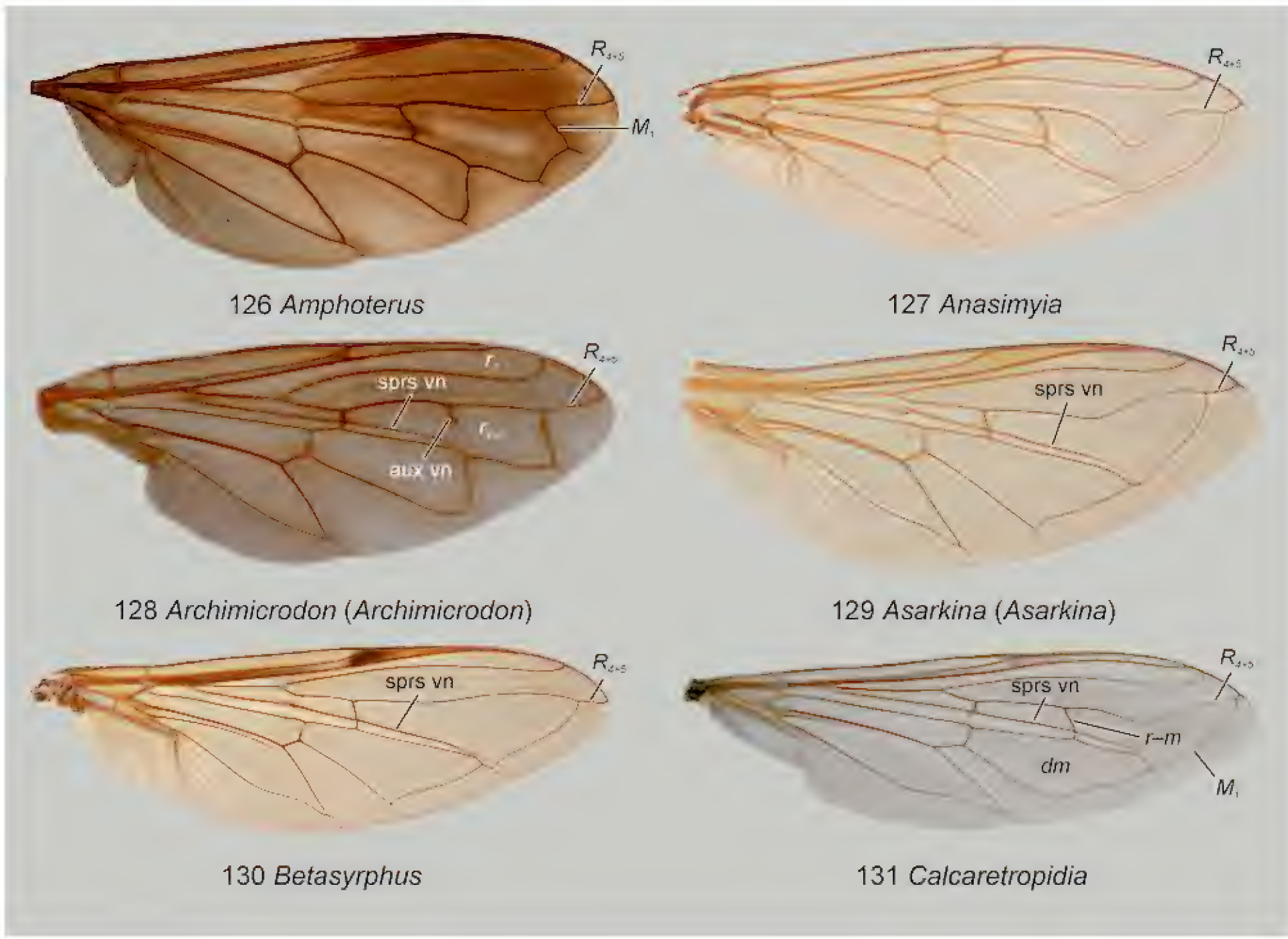
Figs 60.120–125. Wings of Syrphidae (dorsal views): (120) *Eristalis* (*Eristalis*) *tenax* (L.); (121) *Afromicrodon* sp.; (122) *Afrostoma quadripunctatum* Skevington, Thompson & Vockeroth; (123) *Afrosyrphus varipes* Curran; (124) *Allobaccha* sp.; (125) *Allograpta* sp.

Abbreviations: A_1 – first branch of anal vein; al – alula; *bc* – basal costal cell; *bm* – basal medial cell; *br* – basal radial cell; *c* – costal cell; *C* – costal vein; *cua* – anterior cubital cell; *CuP* – posterior branch of cubital vein; *cup* – posterior cubital cell; *dm* – discal medial cell; *h* – humeral crossvein; M_1 – first branch of media; *m–cu* – medial–cubital crossvein; R_1 – anterior branch of radius; r_1 – first radial cell; r_{2+3} – second + third radial cell; R_{2+3} – second branch of radius; r_{4+5} – fourth + fifth radial cells; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *sc* – subcostal cell; *Sc* – subcostal vein; sprs vn – spurious vein.

species are often associated with ants' nests, where they probably feed on root aphids, but the larvae and biology of *C. continum* remain unknown.

***Episyrphus* Matsumura** (Syrphinae: Syrphini)**.** A genus of 10 species occurring in the Afrotropical, Australasian, Oriental and Palaearctic Regions. Seven species occur in the Afrotropics distributed through the entire Afrotropical Region. *Episyrphus* (Fig. 57) are small- to medium-sized (length: 8–12 mm) flies, with a greenish thorax and orange abdomen with double black fasciae, closely spaced black maculae at the wing margin and a setulose anterior anepisternum and setulose metasternum. Habitat types include forests and their margins mountain shrublands and heathlands. Adults often occur on flowers of *Ageratum conyzoides*, *Galinsoga parviflora* Cav. (Asteraceae), *Helichrysum forskalii*, *Sida acuta* Burm.f (Malvaceae) and *Solanum nigrum* L. (Solanaceae) (Classen *et al*. 2020). Larvae are predatory on Sternorrhyncha. Identification keys to Afrotropical species were provided by Curran (1938*b*) (as *Syrphus*) and Vockeroth (1973).

***Eristalinus* Rondani** (Eristalinae: Eristalini)**.** An Old World genus of *ca* 75 species, occurring in the Afrotropical, Australasian, Oriental and Palaearctic Regions, with a few species introduced into the New World (California and Florida, U.S.A.). The genus is divided into six subgenera: *Eristalinus sensu stricto* (including the synonym *Lathyrophthalmus* Mik; Figs 7, 58), with 39 species in the Afrotropics; *E.* (*Eristalodes* Mik) (Fig. 59), with 12 Afrotropical species; *E.* (*Helophilina* Becker) endemic to the Afrotropics, with a single small, metallic green species, *E.* (*H.*) *smaragdinus* (Macquart, 1842) (Fig. 60); *E.* (*Merodonoides* Curran) (Fig. 61) with seven species, six of which are endemic to the Afrotropics, characterised by the swollen hind femur (Thompson 2019*b*); and *E.* (*Oreristalis* Séguy) (Fig. 62), with four brilliant metallic bluish to green species with a shiny mesonotum, all endemic to the Afrotropical Region. *Eristalinus* (Figs 7, 58–62) are small- to large-sized (length: 4–16 mm) flies, most of which are honeybee-mimics with maculate (Fig. 58) and/or fasciate (Fig. 59) eyes. They occur in a wide variety of habitat types, including open grasslands, shrublands, river



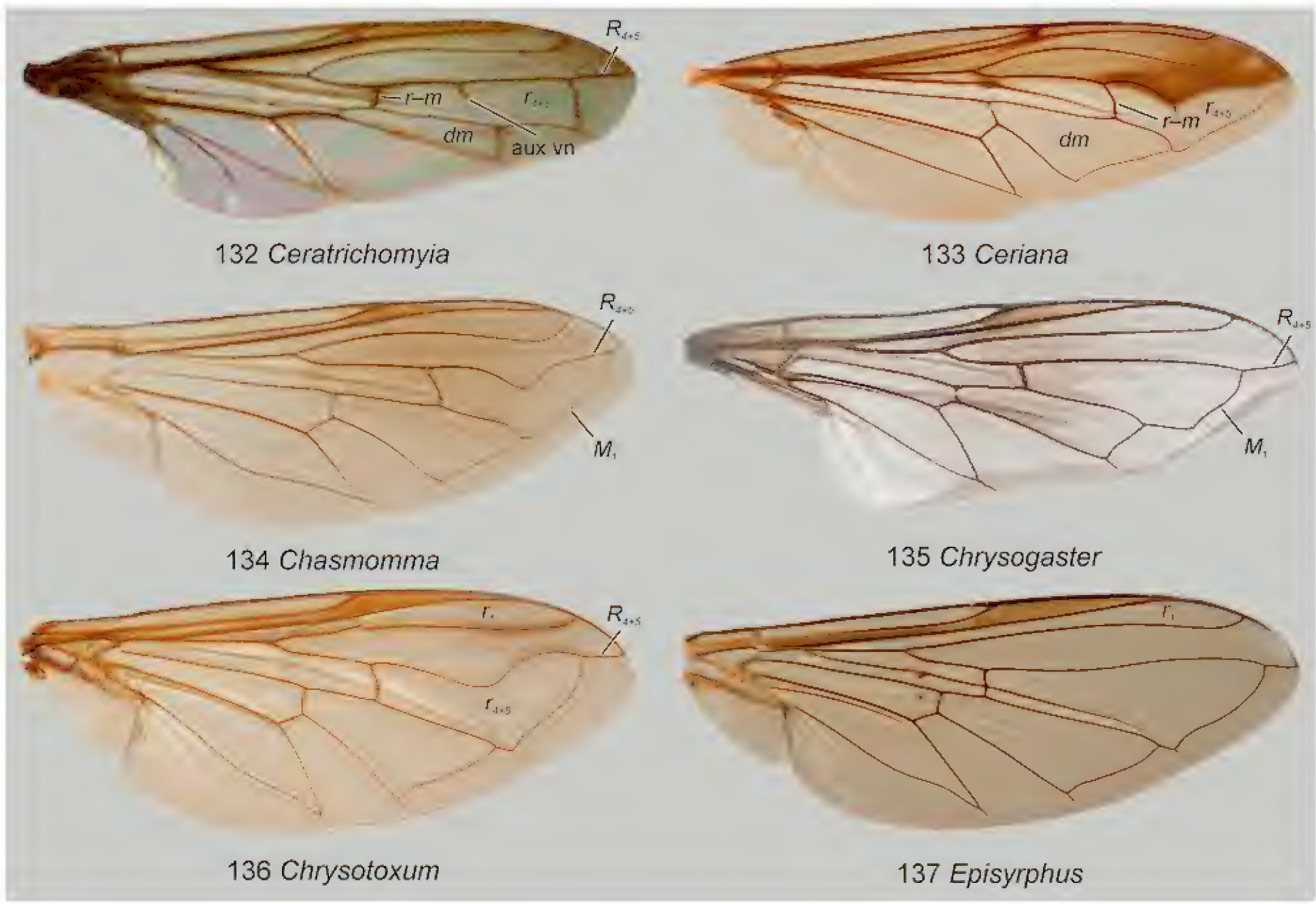
Figs 60.126–131. Wings of Syrphidae (dorsal views): (126) *Amphoterus braunsi* Doesburg; (127) *Anasimyia* sp.; (128) *Archimicrodon* (*Archimicrodon*) sp.; (129) *Asarkina* (*Asarkina*) sp.; (130) *Betasyrphus* sp.; (131) *Calcaretropidia* sp.

Abbreviations: aux vn – auxiliary vein; *dm* – discal medial cell; M_1 – first branch of media; r_1 – first radial cell; r_{4+5} – fourth + fifth radial cells; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; sprs vn – spurious vein.

valleys, forest margins, wetlands, river margins, lake shores and small temporary waterbodies, even in urban areas. Adults can occur far from suitable larval habitat types. Adult *Eristalinus* exhibit a preference for composite flowers of Asteraceae (*Berkshiria*, *Bidens pilosa* L., *Chrysanthemum*, *Senecio* and *Emilia*) or Euphorbiaceae (Classen *et al*. 2020). The semiaquatic larvae feed on bacteria in shallow water with rotting organic matter. Biology and larval stages otherwise remain unknown. An identification key to about half of the Afrotropical species was provided by Curran (1939*b*) (as *Eristalodes* and *Lathyrophthalmus*).

Eristalis **Latreille** (Eristalinae: Eristalini)**.** A mainly Holarctic genus of *ca* 96 species occurring in all zoogeographical regions, except Antarctica. *Eristalis*, including the subgenus *E.* (*Eoseristalis* Kanervo), is largely northern temperate, with a few species occurring in the Neotropical and Oriental Regions. Seven species of *E.* (*Eoseristalis*) occur in the Afrotropics and are known from Bioko Is. (Equatorial Guinea), Côte d'Ivoire, Democratic Republic of Congo, Guinea-Bissau and South Africa. The subgenus *Eristalis sensu stricto* is restricted to the Afrotropical, Oriental and Palaearctic Regions (two species), but *E.* (*E.*) *tenax* has been introduced into the New World and Australasia and is the only species of the subgenus to occur in the Afrotropics (Réunion Is., Saint Helena Is. and South Africa). *Eristalis* (Fig. 63) are medium- to large-sized (length: 12–16 mm) flies, often brownish to orange coloured, honeybee-mimics, but some species are also mimics of stingless bees and have long dense setulae on the hind legs. Habitat preferences are diverse and *E. tenax* occurs in a variety of open habitats and several *E.* (*Eoseristalis*) species inhabit forests and have been recorded from coffee plantations. Adults occur on many different flowers in the herb and shrub layer. Larvae are the so-called "rat-tailed maggots" (Fig. 213), which develop submerged in waterbodies rich in organic matter, where they feed on micro-organisms. Biology and larval stages of species other than *E. tenax*, remain largely unknown. An identification key to Afrotropical species was provided by Curran (1939*b*).

Eumerus **Meigen** (Eristalinae: Eumerini)**.** A widely distributed genus of nearly 300 described species, occurring in the Afrotropical, Oriental Palaearctic and Australasian Regions, with high species diversity in the Mediterranean province. Some species have also been introduced into the Australasian,

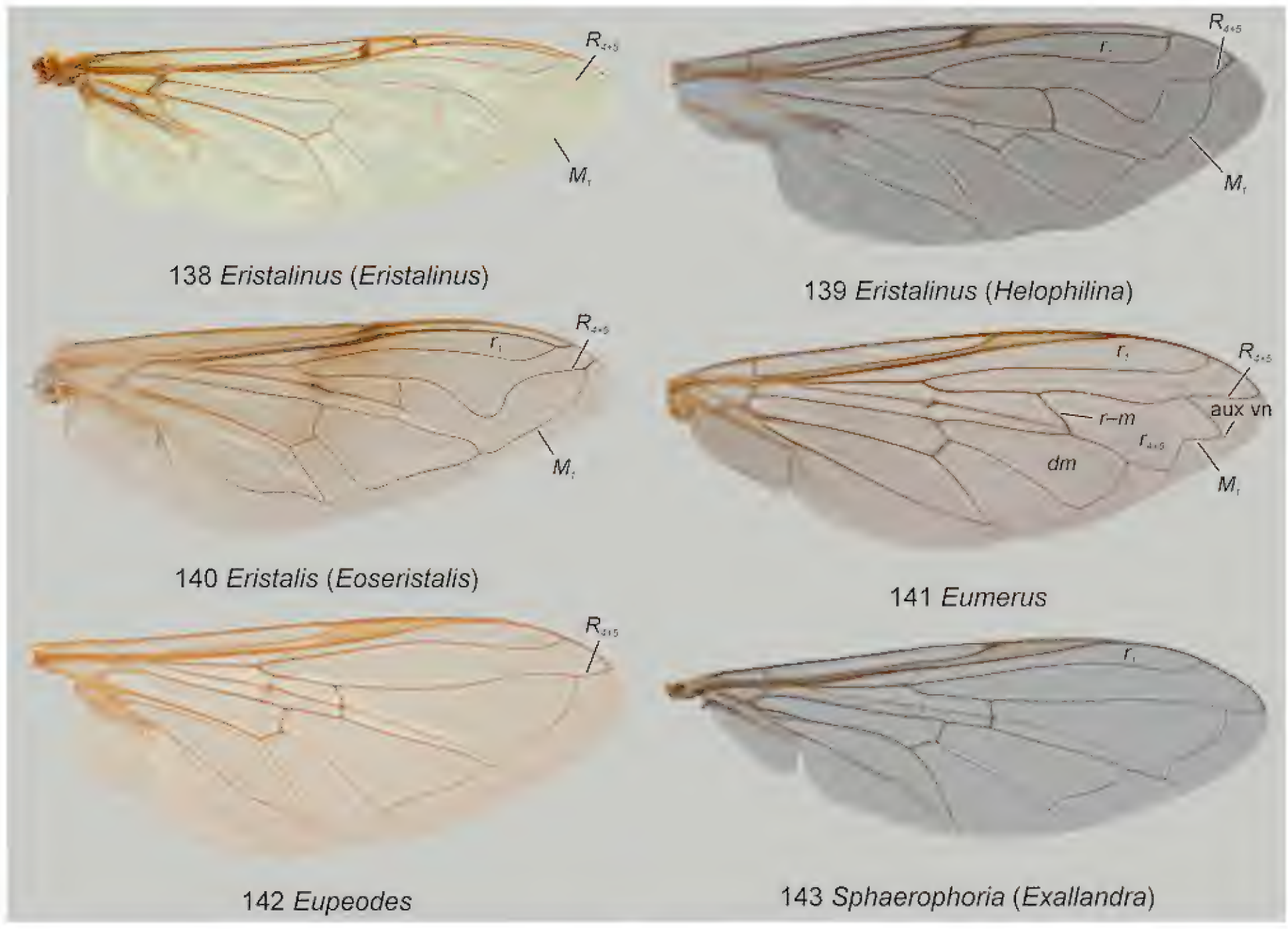


Figs 60.132–137. Wings of Syrphidae (dorsal views): (132) *Ceratrichomyia* sp.; (133) *Ceriana* sp.; (134) *Chasmomma* sp.; (135) *Chrysogaster* sp.; (136) *Chrysotoxum continum* Bezzi; (137) *Episyrphus trisectus* (Loew).

Abbreviations: aux vn – auxiliary vein; *dm* – discal medial cell; M_1 – first branch of media; r_1 – first radial cell; r_{4+5} – fourth + fifth radial cells; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein.

Nearctic and Neotropical Regions. *Eumerus* (Figs 8, 64) are small- to medium-sized (length: 5–10 mm), compact flies, often with greyish fasciae on the otherwise dark or reddish abdomen. Species of this genus have a characteristic wing venation, with a recessive M_1 vein (Fig. 141) and lack long setulae on the lower calypter (Fig. 181) (the latter character distinguishing the genus from *Megatrigon*, Figs 72, 180). Species occur in open, semi-humid to dry grasslands, open forests and savanna, karoo vegetation and semi-desert, with *Aloe* (Asphodeloideae) species and rocky outcrops with sparse vegetation. Several species also occur in urban gardens, parks and nurseries. *Eumerus* species mainly visit flowers of Asteraceae (e.g., *Conyza* and *Senecio*), Euphorbiaceae and other flowers with relatively open nectar sources (A. Ssymank, pers. obs.). Adults often occur in the vicinity of larval host-plants, usually resting on more or less bare ground or on nearby vegetation. They are rapid flyers and fly low among open vegetation. Larvae are phytophagous in bulbs and plant rhizomes. Some species appear to be associated with *Aloe*. An identification key to 26 Afrotropical species was provided by Curran (1938*a*) and to 12 species from Oman, United Arab Emirates and Yemen by Smit *et al*. (2017). Leif Lyneborg (1932–2006) left an unfinished identification key, in which he included 74 undescribed species.

***Eupeodes* Osten Sacken** (Syrphinae: Syrphini)**.** A virtually cosmopolitan genus of 90 species, occurring in all zoogeographical regions, but absent from New Zealand and Antarctica. Highest species diversity occurs in northern temperate zones. Three species occur in the Afrotropics: *E. corollae* (F., 1794), which is widespread in the region; *E. nuba* (Wiedemann, 1830), described from Sudan and also occurs in United Arab Emirates (Smit *et al*. 2017) (but otherwise a Mediterranean species); and *E. ohmi* Kassebeer, 2000, endemic to the Mascarene Is. (described from Réunion Is.). *Eupeodes* (Figs 9, 65) are small- to medium-sized (length: 7–12 mm) flies, with a shiny thorax and yellow fasciae on the abdomen, yellow face, bare eyes and black maculae on the abdominal sternites. Adults are frequent flower visitors on a variety of herbaceous



Figs 60.138–143. Wings of Syrphidae (dorsal views): (138) *Eristalinus* (*Eristalinus*) sp.; (139) *Eristalinus* (*Helophilina*) *smaragdinus* (Macquart); (140) *Eristalis* (*Eoseristalis*) sp.; (141) *Eumerus* sp.; (142) *Eupeodes corollae* (F.); (143) *Sphaerophoria* (*Exallandra*) *cinctifacies* (Speiser).

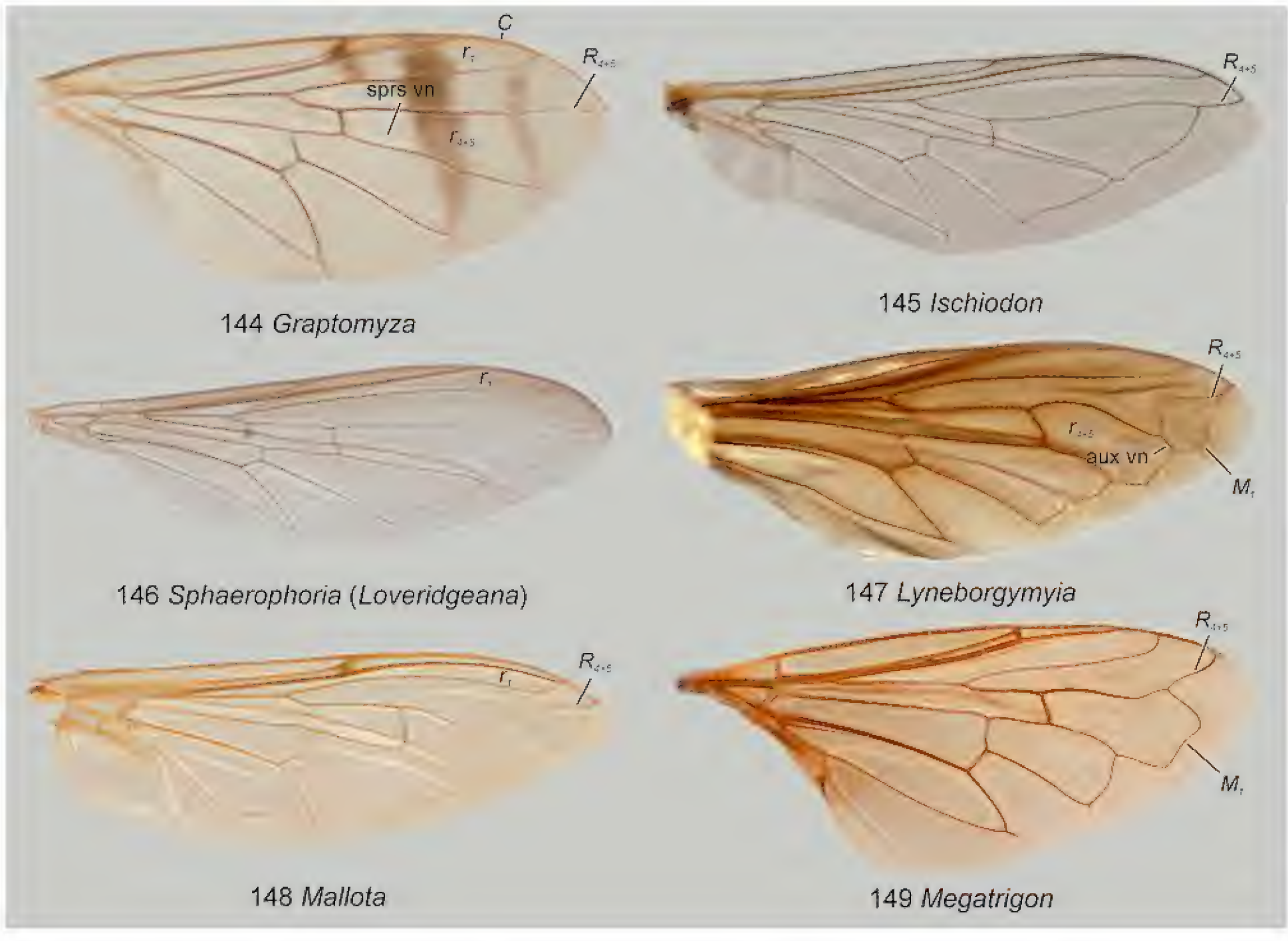
Abbreviations: aux vn – auxiliary vein; *dm* – discal medial cell; M_1 – first branch of media; r_1 – first radial cell; r_{4+5} – fourth + fifth radial cells; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein.

plants. Larvae are predatory on Sternorrhyncha. An identification key to Afrotropical species is not available.

***Exallandra* Vockeroth** (Syrphinae: Syrphini)**.** An endemic monotypic genus with the single species, *E. cinctifacies* (Speiser, 1910), described from Tanzania, but further recorded from Democratic Republic of Congo, Kenya, Liberia and South Africa. *Exallandra cinctifacies* (Fig. 66) is a small-sized (length: 6–8 mm), slender, yellow and black fly, with the lateral yellow vittae on the scutum not extending beyond the transverse suture and a well-developed subscutellar fringe. Biology and immature stages remain unknown.

***Graptomyza* Wiedemann** (Eristalinae: Volucellini)**.** An Old World tropical genus of 92 described species, occurring in the Afrotropical, Australasian, Oriental and Palaearctic Regions. In the Afrotropics, 20 species have been described and several undescribed species are known. The most abundant species, *G. triangulifera* (Bigot, 1883), is widespread across the Afrotropics, but most other species have more localised distributions. *Graptomyza* (Fig. 67) are small- to medium-sized (length: 6–10 mm), yellow and black, or dark metallic flies, often with patterned wings (Fig. 144), a plumose antennal arista, a "snout", a medial rounded excavation in the scutellum (Fig. 109) and the eyes are dichoptic in males. Habitat types mainly comprise lowland rainforests to mountain cloud forests, but also fruit tree plantations. Flower visits are known from *Euphorbia engleri* Pax (Euphorbiaceae) (A. Ssymank, pers. obs.). Known larvae are saprophagous in decaying fruits and roots and *G. triangulifera* larvae develop in rotten Avocado fruits, *Persea americana* Mill. (Lauraceae) (A. Ssymank, pers. obs.). Aracil *et al*. (2019) described the third-instar larva and puparium of *G. signata* (Walker, 1860). Biology and immature stages of Afrotropical species otherwise remain unknown. An identification key to Afrotropical species was provided by Whittington (1992, 1994*b*).

***Ischiodon* Sack** (Syrphinae: Syrphini)**.** A small genus of four species: one widespread Australasian/Oriental species,



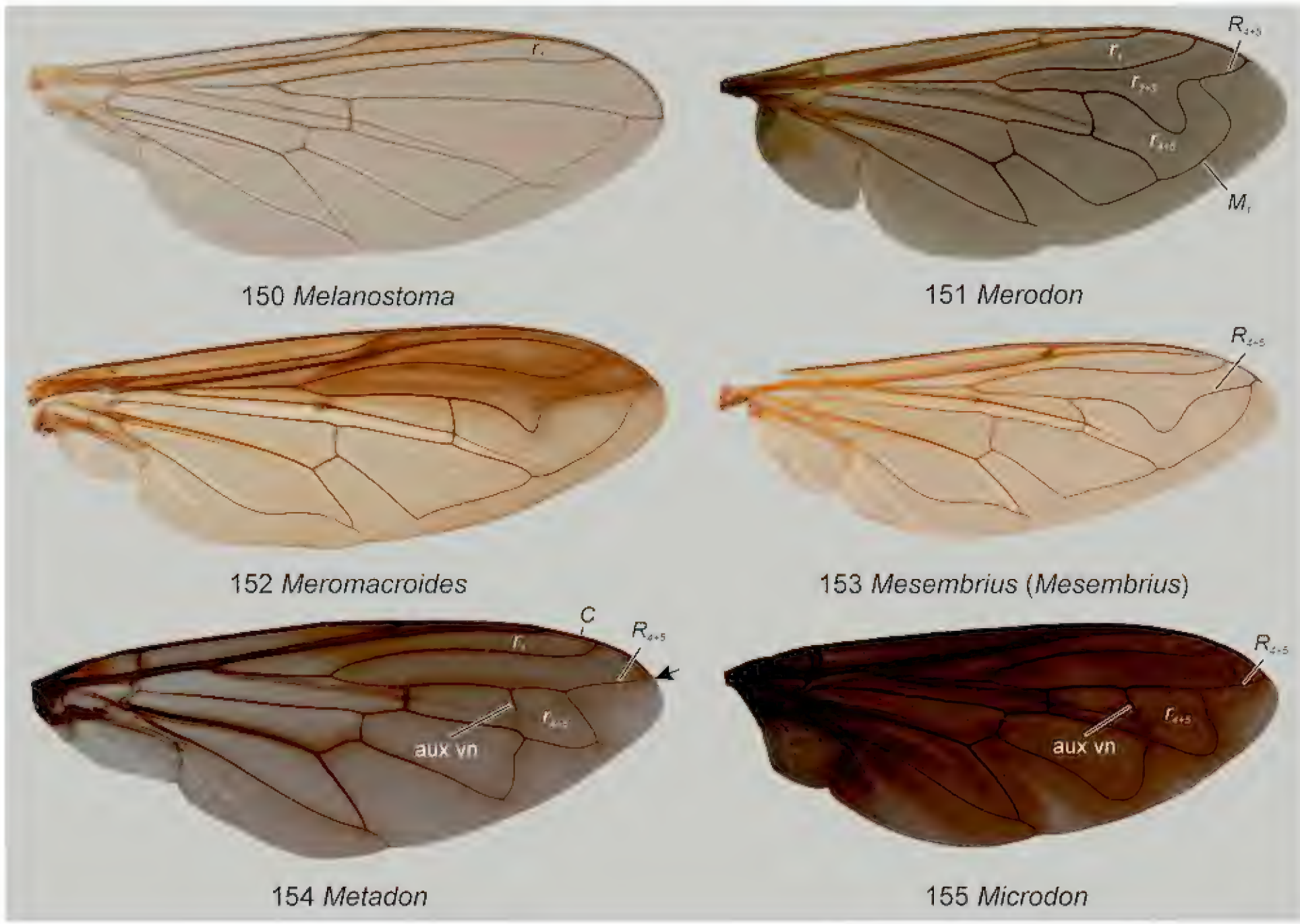
Figs 60.144–149. Wings of Syrphidae (dorsal views): (144) *Graptomyza* sp.; (145) *Ischiodon aegyptius* (Wiedemann); (146) *Sphaerophoria* (*Loveridgeana*) *beattiei* Doesburg & Doesburg; (147) *Lyneborgymyia magnifica* Doczkal & Pape; (148) *Mallota* sp.; (149) *Megatrigon* sp.

Abbreviations: aux vn – auxiliary vein; *C* – costal vein; M_1 – first branch of media; r_1 – first radial cell; r_{4+5} – fourth + fifth radial cells; R_{4+5} – third branch of radius; sprs vn – spurious vein.

I. scutellaris (F., 1805), which was recently recorded from United Arab Emirates (Mengual 2018), one widespread Afrotropical (*I. aegyptius* (Wiedemann, 1830)), one endemic to Madagascar (*I. astales* Mengual, 2018) and one endemic to Cabo Verde (*I. feae* Bezzi, 1912). *Ischiodon* (Fig. 68) are medium-sized (length: 9–12 mm) flies, with bright lateral vittae on the scutum extending to the scutellum. They occur in a wide range of open and semi-open habitat types, such as grasslands, heathlands, savanna, open moist to wet forests, rock outcrops, agricultural fields and urban habitats, such as gardens, parks and plant nurseries. Adults occur on a wide range of herbs, e.g., *Euphorbia millii* Des Moul. (Euphorbiaceae), Commelinaceae, Asteraceae (e.g., *Tridax procumbens* L.), also on medicinal and cultivated plants, such as *Richardia scabra* L. (Rubiaceae) and *Pisidium guajava* L. (Myrtaceae) (A. Ssymank, pers. obs.). Larvae feed on Aphididae and have a strong potential in biocontrol and integrated pest management. An identification key and redefinition of the genus was provided by Mengual (2018).

***Loveridgeana* Doesburg & Doesburg** (Syrphinae: Syrphini)**.** An endemic, monotypic genus with the single species, *L. beattiei* Doesburg & Doesburg, 1976, described from Saint Helena Is. (Doesburg & Doesburg 1976). *Loverdigeana beattiei* (Fig. 69) is a small- to medium-sized (length: 8–11 mm) fly, characterised by the yellow lateral vitta on the scutum that extends to the scutellum, the large male terminalia, the lack of a subscutellar setula fringe on the thorax and the eyes are dichoptic in males. Adults have been collected from flowers of *Ageratum* (Asteraceae), *Commidendron robustum* (Roxb.) DC. (Asteraceae), *Lilium longiflorum* Thunb. (Liliaceae), *Rubus* (Rosaceae) and *Daucus* (Apiaceae) (Doesburg & Doesburg 1976). The biology and immature stages of the species otherwise remain unknown.

***Lyneborgimyia* Doczkal & Pape** (Eristalinae: Eumerini)**.** An endemic monotypic genus, with the single species, *L. magnifica* Doczkal & Pape, 2009, described from the Uzungwa (Eastern Arc) Mountains of Tanzania. Only the male holotype and one female specimen from Uluguru (Eastern Arc) Mountains



Figs 60.150–155. Wings of Syrphidae (dorsal views): (150) *Melanostoma* sp.; (151) *Merodon* sp.; (152) *Meromacroides meromacriformis* (Bezzi); (153) *Mesembrius* (*Mesembrius*) sp.; (154) *Metadon* sp. (arrow indicates extent of costal vein); (155) *Microdon* (*Microdon erythros* species-group) sp.

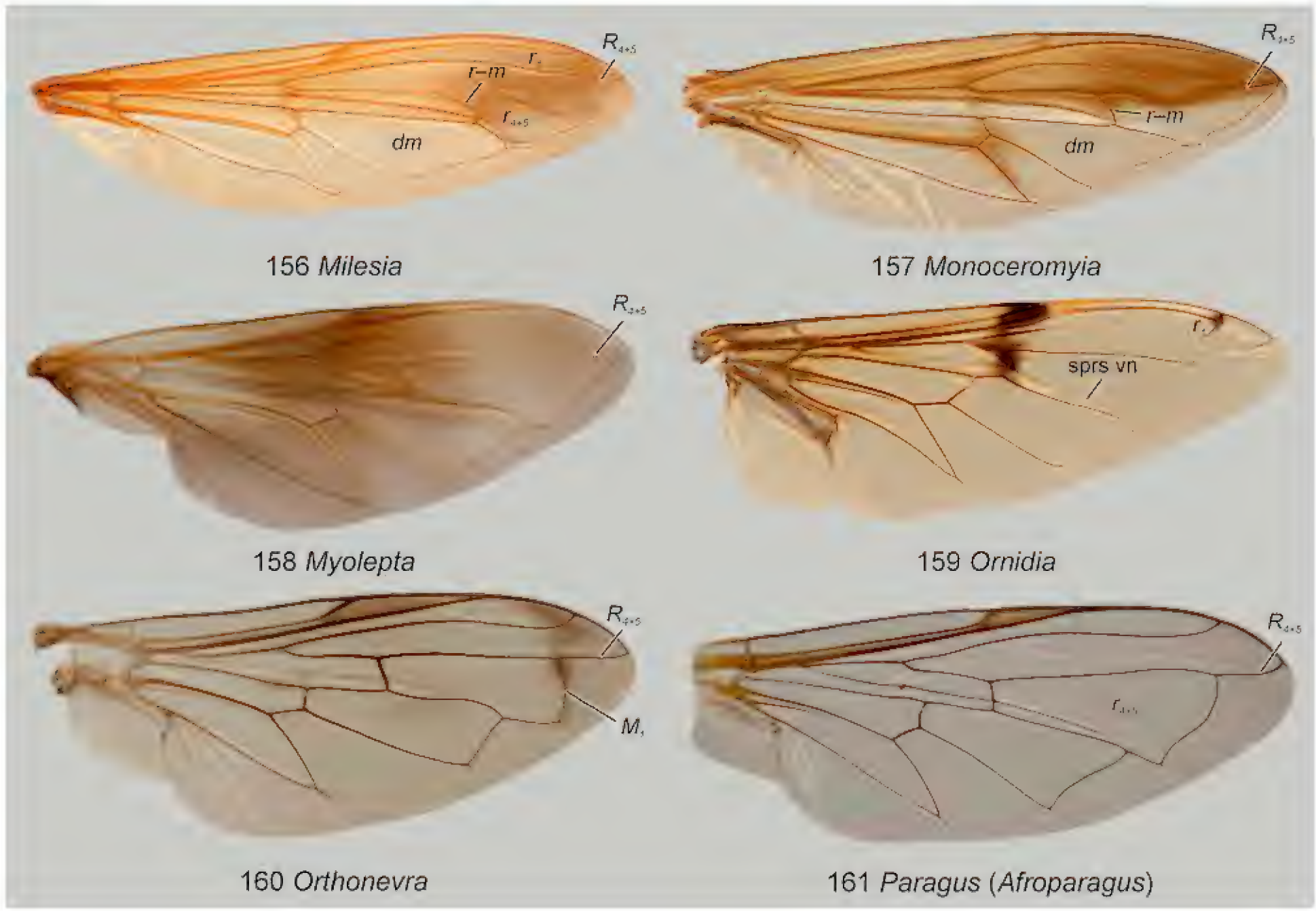
Abbreviations: aux vn – auxiliary vein; *C* – costal vein; M_1 – first branch of media; r_1 – first radial cell; r_{2+3} – second + third radial cell; r_{4+5} – fourth + fifth radial cells; R_{4+5} – third branch of radius.

are known. *Lyneborgimyia magnifica* (Fig. 70) is a large-sized (length: *ca* 18 mm) fly, with the abdomen clothed in dense golden setulae, the greatly enlarged male terminalia and a characteristic wing venation, with cell r_{4+5} largely (female) or entirely (male) divided by a crossvein (Fig. 147). Biology and immature stages of the species remain unknown.

***Mallota* Meigen** (Eristalinae: Eristalini)**.** A mainly Palaearctic and Nearctic genus of *ca* 70 described species, with extensions into the Afrotropical, Neotropical (south to Brazil) and Oriental (Indonesia) Regions. Six species occur in the Afrotropics, widely distributed throughout the Afrotropical Region. Afrotropical *Mallota* is probably a paraphyletic group and requires taxonomic revision. *Mallota* (Fig. 71) are medium- to large-sized (length: 11–17 mm) flies (Fig. 71), with a sinuate R_{4+5} wing vein (Fig. 148). *Mallota* are honeybee-mimics and often occur in tree canopies, above shrubs or hovering in front of tree rot holes. Typical habitat types include forests or forest margins with numerous dead trees and rot holes. In the Palaearctic Region, the "rat-tailed maggots" occur in humid rot holes in trees. Biology and immature stages of Afrotropical species remain unknown. An identification key to Afrotropical species was provided by Curran (1939*b*) (partially as *Eristalis* and *Senaspis*).

***Megatrigon* Johnson** (Eristalinae: Eumerini)**.** An endemic genus of 15 species, which some authors, e.g., Smith & Vockeroth (1980: 497), previously considered a synonym of *Eumerus*. Doczkal *et al*. (2016) re-established the genus however. *Megatrigon* is divided into three species-groups: the *M. argenteus*-group (11 species); the *M. nivalis*-group (1); and the *M. sexfasciatus*-group (3). The known distribution is largely South Africa. *Megatrigon* (Fig. 72) are small- to medium-sized (length: 7–11 mm) flies, resembling *Eumerus* (Figs 8, 64), but with long setulae dorsally on the lower calypter (Fig. 180), striae on the hind femur and differences in the male terminalia. Larvae are phytophagous, as noted for *Eumerus* (above), probably in bulb plants, but the biology remains largely unknown. An identification key was provided by Doczkal *et al*. (2016).

***Melanostoma* Schiner** (Syrphinae: Syrphini)**.** A virtually cosmopolitan genus of 75 species, occurring in all zoogeographical regions, except Antarctica, but restricted to the extreme



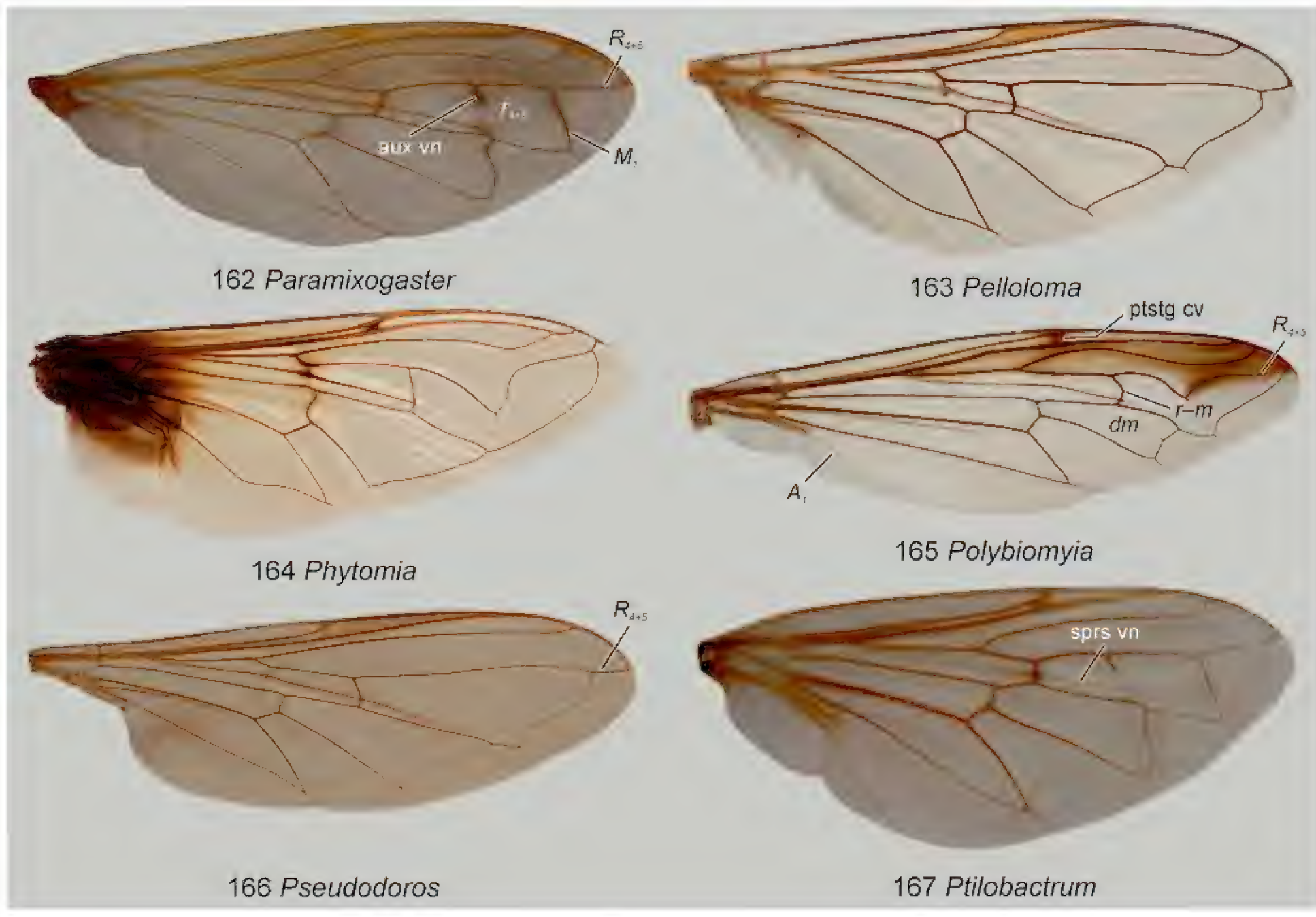
Figs 60.156–161. Wings of Syrphidae (dorsal views): (156) *Milesia* sp.; (157) *Monoceromyia* sp.; (158) *Myolepta* sp.; (159) *Ornidia obesa* (F.); (160) *Orthonevra* sp.; (161) *Paragus* (*Afroparagus*) sp.

Abbreviations: *dm* – discal medial cell; M_1 – first branch of media; r_1 – first radial cell; r_{4+5} – fourth + fifth radial cells; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; sprs vn – spurious vein.

northern part of the Neotropics (south to Chiapas). Twenty-three species are widely distributed throughout the Afrotropics. *Melanostoma* (Fig. 73) are small- to medium-sized slender (length: 6–11 mm) flies, with a black face and abdomen, often with yellow to orange maculae or fasciae. The genus is differentiated from closely related genera by the greatly reduced thoracic metasternum (Fig. 119). Species occur in a wide variety of habitat types, from forests to grasslands and wetlands (including anthropogenic habitats), usually with a preference for moist to wet habitats, but are absent from very dry habitats. While extralimital species tend to visit flowering grasses and sedges, Afrotropical species visit a wider variety of flowers, mostly of herbaceous plants (e.g., *Begonia* (Begoniaceae), *Cynoglossum* (Boraginaceae), *Galinsoga* (Asteraceae), *Mimulopsis* (Acanthaceae), *Plectranthus* (Lamiaceae), *Solanum* (Solanaceae), *etc.*) and shrubs (e.g., *Euphorbia* and *Xymalos*) (A. Ssymank, unpubl.). Larvae are predatory on Sternorrhyncha. An identification key to six Afrotropical species was provided by Curran (1938*b*) and Dirickx (2001) provided an identification key to Malagasy species.

***Meliscaeva* Frey** (Syrphinae: Syrphini)**.** A largely Oriental genus of 22 species, with four species in the Palaearctic Region and one species in the Holarctic Realm. In the Afrotropics, only *M. auricollis* (Meigen, 1822) has been reported from Cabo Verde (Barkemeyer 2002). *Meliscaeva* are small- to medium-sized (length: 6–11 mm) flies, with a setulose anterior anepisternum, a bare metasternum and a series of minute black maculae on the posterior margin of the wing. Palaearctic *Meliscaeva* often occur on a variety of flowers in forests, but the biology and larval stages of *M. auricollis* remain unknown, although larvae of extralimital species are predatory on Sternorrhyncha.

***Merodon* Meigen** (Eristalinae: Eumerini)**.** A genus of 160 species, largely restricted to the western Palaearctic, with a few species also occurring in the Afrotropical and northern Oriental Regions. Some European species have been introduced to other regions. Twelve species are currently known from the Afrotropics, but there are a comparable number of species awaiting description (A. Vujić & S. Radenković, pers. comms. 2019, 2020). The genus is distributed in Kenya, Malawi, South



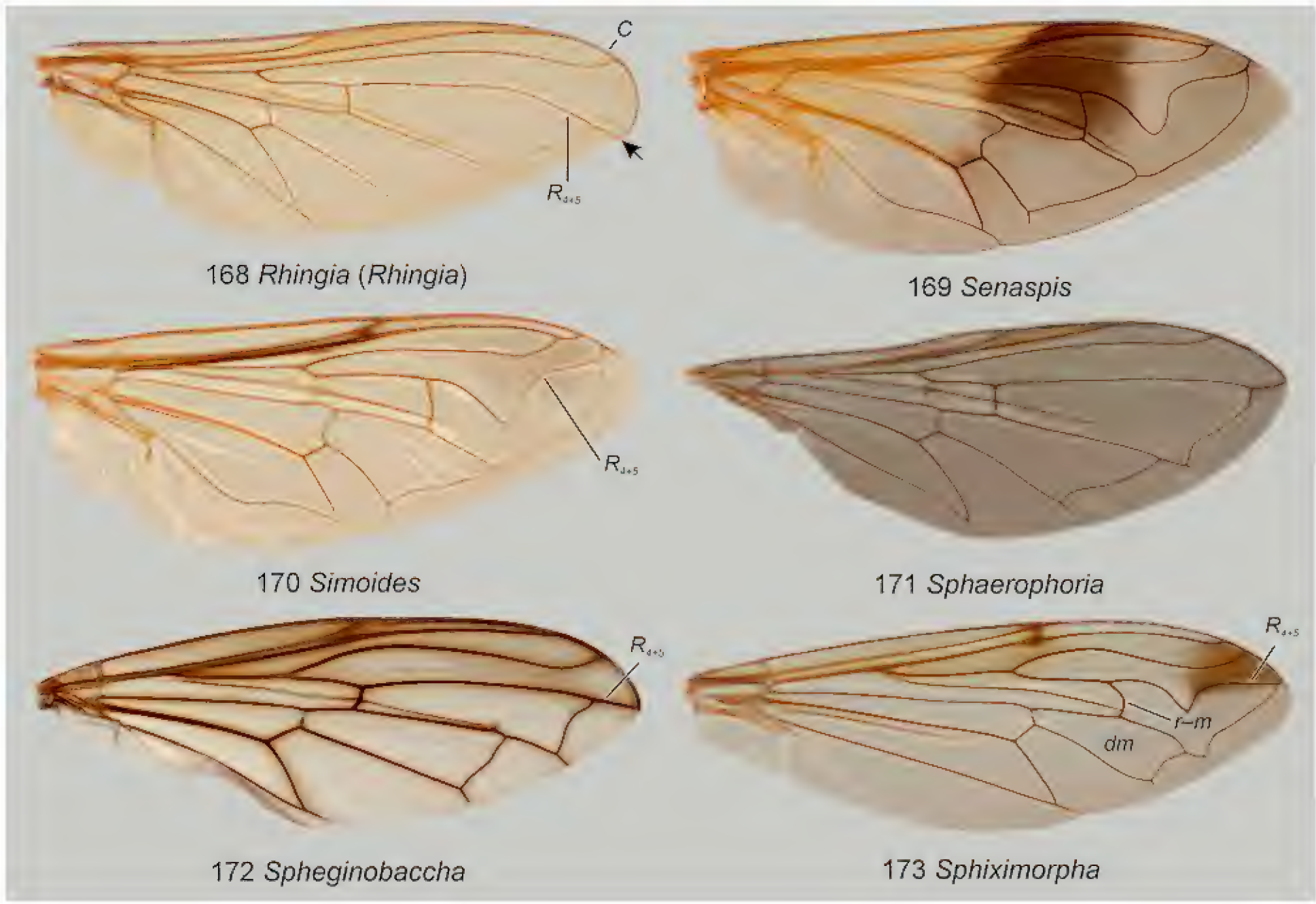
Figs 60.162–167. Wings of Syrphidae (dorsal views): (162) *Paramixogaster* sp.; (163) *Pelloloma nigrifacies* Vockeroth; (164) *Phytomia* sp.; (165) *Polybiomyia* sp.; (166) *Pseudodoros nigricollis* Becker; (167) *Ptilobactrum neavei* Bezzi.

Abbreviations: A_1 – first branch of anal vein; aux vn – auxiliary vein; *dm* – discal medial cell; M_1 – first branch of media; ptstg cv – pterostigma crossvein; r_{4+5} – fourth + fifth radial cells; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; sprs vn – spurious vein.

Africa and Zimbabwe. *Merodon* (Fig. 74) are medium-sized (length: 10–14 mm), stout flies that resemble honey or bumblebees. The genus is recognised by the relatively small wing and head (Fig. 74), the strongly sinuate R_{4+5} wing vein (Fig. 151) and the thickened hind femur, with an apicoventral triangular expansion (Fig. 188). The genus occurs in grasslands and on vegetation in dry, sparsely vegetated rocky slopes or cliffs. Adults are rarely observed on flowers, but females of some species visit Asteraceae (*e.g.*, *Heteromma* and *Senecio*). Adults are more often observed flying in low vegetation or alighting on small, bare patches of soil. Larvae are endophytophagous in bulbs of Liliaceae *sensu lato*, *e.g.*, *Gladiolus*, *Merwillea* (*Scilla*) and *Uriginea* (A. Ssymank, pers. obs.), but the immature stages and biology otherwise remain unknown for the majority of Afrotropical species. An identification key to Afrotropical species was provided by Curran (1939*a*) and by Radenković *et al.* (2018), for the five species of the *M. melanocerus* subgroup.

***Meromacroides* Curran** (Eristalinae: Eristalini)**.** An endemic monotypic genus, with the single species, *M. meromacriformis* Bezzi, 1915, described from South Africa. *Mermomacroides meromacriformis* (Fig. 75) is a medium- to large-sized (length: *ca* 14 mm) fly, with a greatly swollen hind femur, apical brown maculae at the wing tip and cell r_1 bulbous apically (Fig. 152). Biology and immature stages of the species remain unknown. Taxonomic and biological notes on the species were provided by Bellingan *et al.* (in press).

***Mesembrius* Rondani** (Eristalinae: Eristalini)**.** An Old World genus of *ca* 58 described species, occurring in the Afrotropical, Australasian, Oriental and southern Palaearctic Regions. Twenty-seven species occur in the Afrotropics, widely distributed in the continental Afrotropics and Madagascar. The four Malagasy species, which have extremely enlarged male terminalia (Fig. 203), have been recognised as a separate subgenus: *M.* (*Vadonimyia* Séguy). *Mesembrius* (Figs 10, 76) are medium- to large-sized (length: 10–20 mm) flies, with a broad abdomen, often with extensive orange or yellow fasciae on the tergites, the thorax often has a longitudinal, pruinescent fascia and hind tarsomere 1 has a tuft of globuliferous setulae basoventrally (Fig. 189). Several species exhibit sexual dimorphism, with males having extensive setulae on the fore leg and often modified hind legs. The genus occurs in moist to wet habitat types, including wetlands, marshes and the margins of small to large rivers,



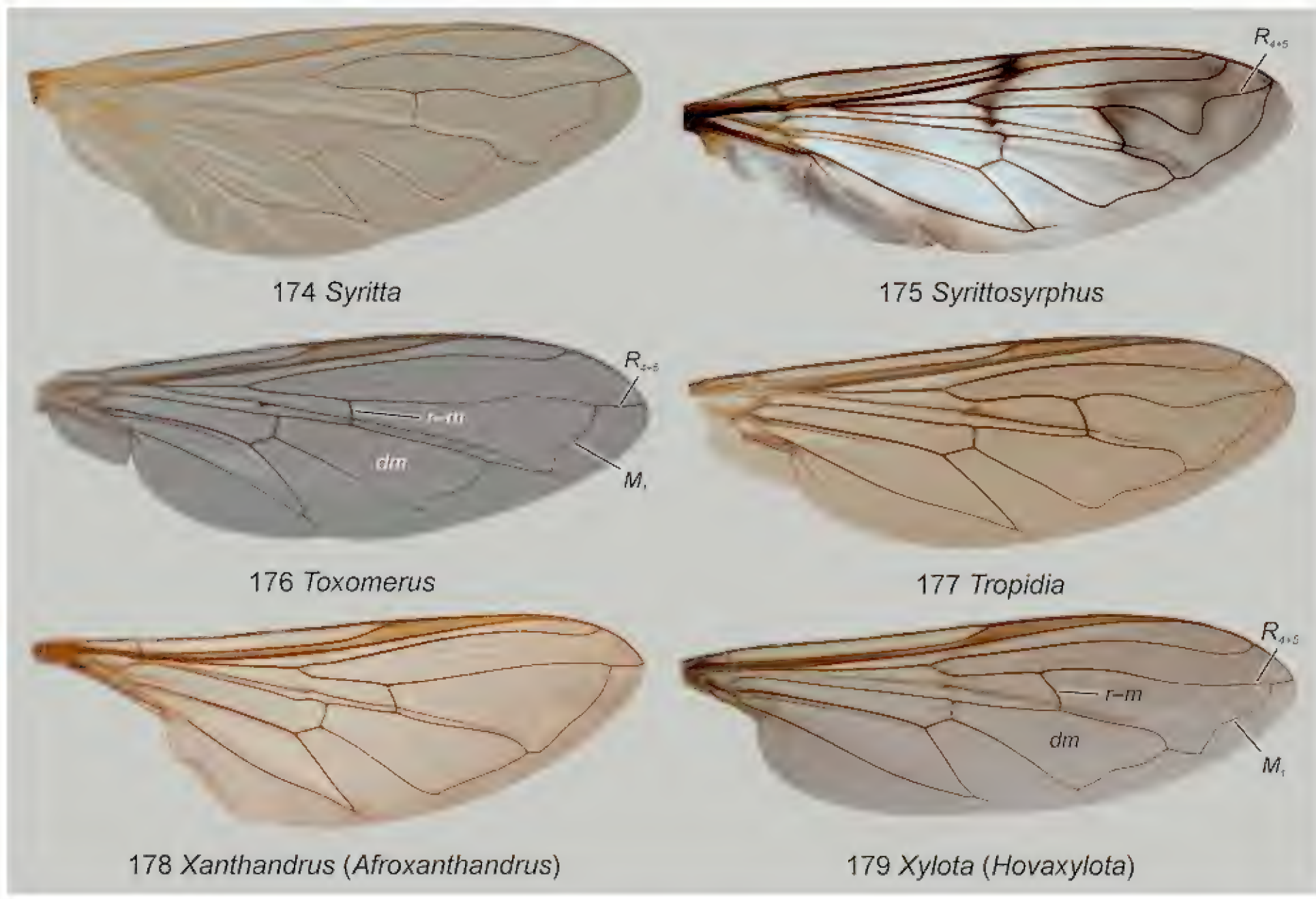
Figs 60.168–173. Wings of Syrphidae (dorsal views): (168) *Rhingia* (*Rhingia*) sp. (arrow indicates extent of costal vein); (169) *Senaspis* sp.; (170) *Simoides* sp.; (171) *Sphaerophoria* sp.; (172) *Spheginobaccha* sp.; (173) *Sphiximorpha* sp.

Abbreviations: *C* – costal vein; *dm* – discal medial cell; R_{4+5} – third branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein.

ponds and lakes. Some species visit flowers of *Typha* (Typhaceae), but also occur on flowers or alight on the leaves of a variety of other plants, e.g., *Ageratum conyzoides* and *Euphorbia heterophylla* L. (Euphorbiaceae) (A. Ssymank, pers. obs.). Larvae are aquatic "rat-tailed maggots". An identification key to Afrotropical species was provided by Curran (1939*b*) and Hippa (1985*b*) provided an identification key to species of the subgenus *M*. (*Vadonimyia*). An identification key was provided by Jordaens *et al*. (2021).

***Metadon* Reemer** (Microdontinae: Microdontini)**.** An Old World tropical genus with 38 described species occurring in the Afrotropical, Australasian, Oriental and Palaearctic Regions. Fourteen species occur in the Afrotropics, distributed throughout the entire region, with the exception of Madagascar. *Metadon* (Figs 11, 77) are small- to large-sized (length: 7–21 mm), slender to moderately broad flies, with long antennae, wing vein R_{4+5} with an auxiliary vein in cell r_{4+5} (Fig. 154) and the anepisternum almost entirely setulose. Biology and immature stages remain unknown, but larvae probably occur in ants' nests, as do other Microdontinae. An identification key is currently unavailable.

***Microdon* Meigen** (Microdontinae: Microdontini)**.** A virtually cosmopolitan genus of 132 described species, but absent from New Zealand, smaller oceanic islands and Antarctica. Fourteen species occur in the Afrotropics. The genus is probably paraphyletic, but several presumably monophyletic subgroups are recognised, two of which are treated as subgenera. The subgenus *M*. (*Megodon* Keiser) is confined to Madagascar and is known from two species, *M*. (*Me*.) *planitarsus* Keiser, 1971 and *M*. (*Me*.) *stuckenbergi* Keiser, 1971. The subgenus *M*. (*Myiacerapis* Hull) comprises one species, *M*. (*My*.) *villosus* Bezzi, 1915, described from Uganda. All remaining species of *Microdon* not included in these two subgenera are here considered to belong to *Microdon sensu lato*, as the subgenus *Microdon sensu stricto* as defined by Reemer & Ståhls (2013*a*, *b*) is not recorded from the Afrotropics. Two additional species-groups of unknown taxonomic ranking are recognised. The *M. erythros* species-group is represented by two species, *M. erythros* Bezzi, 1908 and *M. luteiventris* Bezzi, 1915, occurring in the equatorial parts of the continental Afrotropics. The *M. tarsalis* species-group comprises one species, *M. tarsalis* Hervé-Bazin, 1913 described from Democratic Republic of Congo. In addition, there are seven Malagasy species



Figs 60.174–179. Wings of Syrphidae (dorsal views): (174) *Syritta flaviventris* Macquart; (175) *Syrittosyrphus opacea* Hull; (176) *Toxomerus floralis* (F.); (177) *Tropidia* sp.; (178) *Xanthandrus* (*Afroxanthandrus*) sp.; (179) *Xylota* (*Hovaxylota*) sp.

Abbreviations: *dm* – discal medial cell; M_1 – first branch of media; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein.

that are not placed in a subgenus or species-group (Reemer & Bot 2015). *Microdon* (Figs 11, 78) are small- to medium-sized (length: 8–16 mm) flies, with a broad abdomen, long antennae, wing vein R_{4+5} with an auxiliary vein in cell r_{4+5} (Fig. 155) and the anepisternum extensively bare ventrally. Extralimital species of the subgenus *Microdon sensu stricto* develop in ants' nests as predators of the ants' brood. The biology of Afrotropical *Microdon* remain unknown, but presumably larvae (Figs 212, 216) are also associated with ants. Hocking (1970) recorded a larva of a "*Microdon* sp. ?" from a nest of the ant *Tetraponera penzigi* (Mayr), but the identity of this larva remains uncertain. *Ceratoconcha schultzei* Simroth, 1907 from South Africa was described as a mollusc by Simroth (1907), based on a larva and although this clearly belongs to the subfamily Microdontinae, it cannot be assigned to a genus at present. An identification key to 26 Afrotropical species of Microdontinae was provided by Curran (1938*a*), only five of which are currently considered to belong to *Microdon*, even though all 26 were then included in that genus.

***Milesia* Latreille** (Eristalinae: Milesiini)**.** A genus of 79 described species occurring in all zoogeographical regions, except Australasia and Antarctica. Five species occur in the Afrotropics, distributed in Central, East and Southern Africa. The genus is divided into those with an open r_1 wing cell (Fig. 156) and the mesonotum without a distinct pruinescent patterns (two species-groups: *M. arnoldi*-group with three species, *M. arnoldi* (Malloch, 1932) recorded from Malawi, South Africa and Zimbabwe, *M. bequaerti* (Doesburg, 1955) from Democratic Republic of Congo and Kenya and *M. overlaeti* (Doesburg, 1955) from Democratic Republic of Congo and Uganda; *M. prolixa*-group with one species, *M. prolixa* Hippa, 1990 from Nigeria) and the *M. afra*-group, with one species, *M. afra* Doesburg, 1955 from Democratic Republic of Congo and Uganda, with a closed r_1 wing cell and the mesonotum with a distinct pruinescent pattern. *Milesia* (Fig. 79) are medium- to large-sized (length: 14–24 mm) flies, with a distinct ventral spur on the male hind femur (Fig. 187). Adults occur in forests, often in the vicinity of suitable breeding sites, such as fallen trees or dead wood. Larvae are saprophagous in rot holes of trees. An identification key to Afrotropical species was provided by Hippa (1985*a*, 1990).

***Monoceromyia* Shannon** (Eristalinae: Cerioidini)**.** A virtually cosmopolitan genus of *ca* 45 described species, 20 of which occur in the Afrotropics, distributed throughout the region. *Monoceromyia* (Figs 12, 80) are medium- to large-sized (length: 14–20 mm) flies, with a distinctly petiolate abdomen (Fig. 201) and the antennae are long with a terminal stylus, inserted on an extended frontal prominence (Fig. 21). They lack a postmetacoxal bridge, wing crossvein *r–m* is positioned at or beyond the middle of wing cell *dm* and they have a moderately sinuose vein R_{4+5} (Fig. 157). Adults are attracted to mud pools in the vicinity of slow-moving streams with lush vegetation (G. Goergen & K. Jordaens, pers. obs.). Larvae develop in decaying plant sap. An identification key to Afrotropical species was provided by Curran (1938*a*) (as *Cerioides*).

***Myolepta* Newman** (Eristalinae: Eristalini)**.** A genus of 41 described species occurring in all zoogeographical regions, except Australasia and Antarctica. Three species occur in the Afrotropical Region: *M. africana* Thompson, 1974, described from Democratic Republic of Congo; *M. similis* Thompson, 1974, described from Uganda; and *M. triangularis* Thompson, 1974, described from Zimbabwe. *Myolepta* (Fig. 81) are small- to medium-sized (length: 8–12 mm) flies, with ventroapical spines on the femora of all legs. Larvae of extralimital species are saprophagous in rotten tree holes, but the biology and immature stages of Afrotropical species remain unknown. An identification key was provided by Thompson (1974).

***Ornidia* Le Peletier & Serville** (Eristalinae: Volucellini)**.** A genus of five species endemic to the Neotropical Region, but one species, *O. obesa*, has been introduced into the Nearctic Region and the Old World tropics (Thompson 1990). In the Afrotropics, the species is distributed in East, Southern and West Africa, Madagascar and all three Mascarene Is. *Ornidia obesa* is a medium-sized (length: 9–11 mm), broad species, easily recognised by its greenish to bluish, sometimes also brownish metallic body (Fig. 82), a face with one medium and two lateral tubercles and a plumose antennal arista (Fig. 32). Habitat types are mostly subtropical lowland to mountain forests, riverine forests, cocoa and other plantations. Adults are fast flyers mimicking tropical bees, males often hover in sunny, open patches of forest. Larvae are saprophagous in a wide variety of decaying

180 *Megatrigon* 181 *Eumerus* 182 *Betasyrphus*

Figs 60.180–182. Calypters of Syrphidae (lateral views): (180) *Megatrigon* sp.; (181) *Eumerus* sp.; (182) *Betasyrphus* sp.

Abbreviations: l calyp – lower calypter; s – setae; u calyp – upper calypter.

183 *Mallota* 184 *Syrittosyrphus* 185 *Senaspis*

186 *Senaspis* 187 *Milesia* 188 *Merodon*

189 *Mesembrius* (*Mesembrius*) 192 *Calcaretropidia*

190 *Eristalinus* (*Eristalinus*) 191 *Eristalinus* (*Merodonoides*) 193 *Tropidia*

194 *Xylota* (*Hovaxylota*) 195 *Syritta* 196 *Betasyrphus* 197 *Ischiodon*

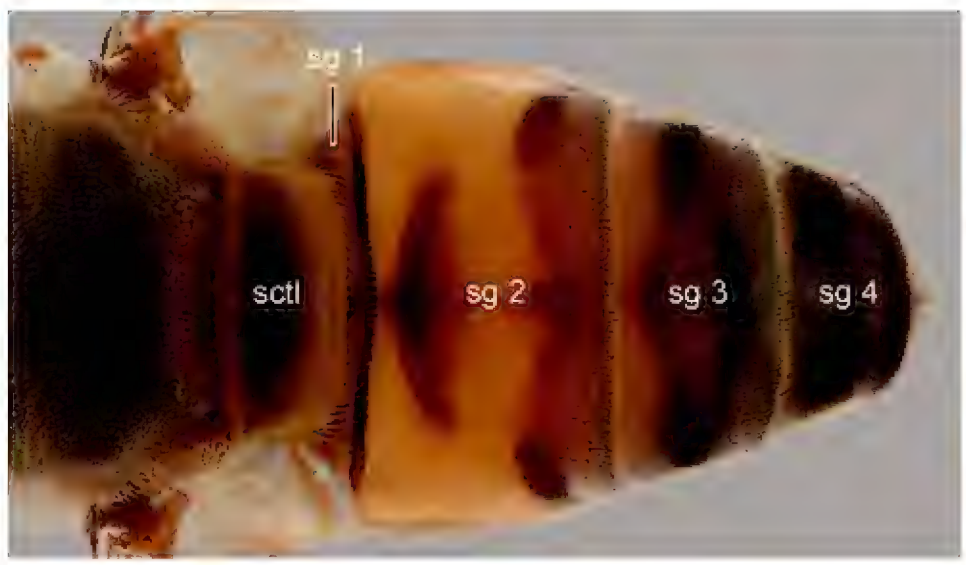
Figs 60.183–197. Hind legs of Syrphidae: (183) *Mallota aperta* (Bezzi), posterior view; (184) same, *Syrittosyrphus opacea* Hull; (185) *Senaspis pennata* (Hervé-Bazin), anterior view; (186) same, *Senaspis* sp.; (187) same, *Milesia* sp.; (188) same, *Merodon* sp.; (189) *Mesembrius* (*Mesembrius*) sp., posterior view; (190) same, *Eristalinus* (*Eristalinus*) sp.; (191) same, *E.* (*Merodonoides*) sp.; (192) *Calcaretropidia* sp., anterior view; (193) *Tropidia* sp., posterior view; (194) same, *Xylota* (*Hovaxylota*) sp.; (195) same, *Syritta* sp.; (196) same, *Betasyrphus* sp.; (197) same, *Ischiodon aegyptius* (Wiedemann).

Abbreviations: cx – coxa; fem – femur; fem exp – femoral expansion; s – seta(e); sp – spine(s); spur – spur; tb – tibia; tsm – tarsomere; tub – tubercle.

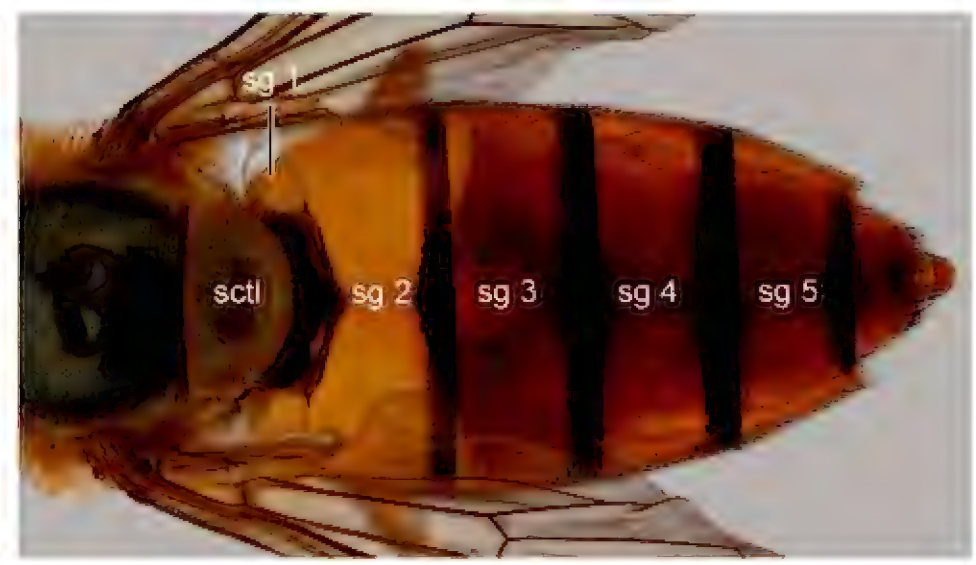
plant materials, from exuding tree sap to decaying flowers, fruits and stems of non-woody plants. They are also associated with mammals, apparently breeding in wounds, dung, carrion and other waste materials, including compost and decaying plant material and vertebrate carrion (Whittington & Rotheray 1997). Accidental myiasis in humans has been rarely reported and larvae may be used diagnostically in forensic entomology (Martins *et al*. 2010).

***Orthonevra* Macquart** (Eristalinae: Brachyopini)**.** A predominantly northern temperate genus, with *ca* 60 described species, occurring in the Afrotropical, Nearctic, Oriental and Palaearctic Regions. Four species occur in the Afrotropics, but their distribution remains unknown. A taxonomic revision is required to unravel the taxonomic relationship with the genus *Chrysogaster*. *Orthonevra* (Fig. 83) are small-sized (length: 4–7 mm), dark, metallic flies, with a shiny abdomen, a characteristic wing venation with a recessive M_1 vein (Fig. 160) and often fasciate or maculate eyes (Fig. 83). The genus occurs in a variety of habitat types, including open wetlands, riverine forests, subtropical rainforests and cloud forests, savannas and shrublands. Flower visiting is known on *Rhus pyroides* (Burch.) Moffett (Anacardiaceae) (A. Ssymank, pers. obs.). Larvae of extralimital species are saprophagous in accumulations of wet, decaying vegetation in slow-moving waterbodies, such as pools and lakes or occur directly on water plants. Adult Afrotropical *Orthonevra* have been observed close to water-filled rot holes or tree roots, where larvae may develop (A. Ssymank, pers. obs.). An identification key to Afrotropical species was provided by Bezzi (1915: 15) (as *Chrysogaster*).

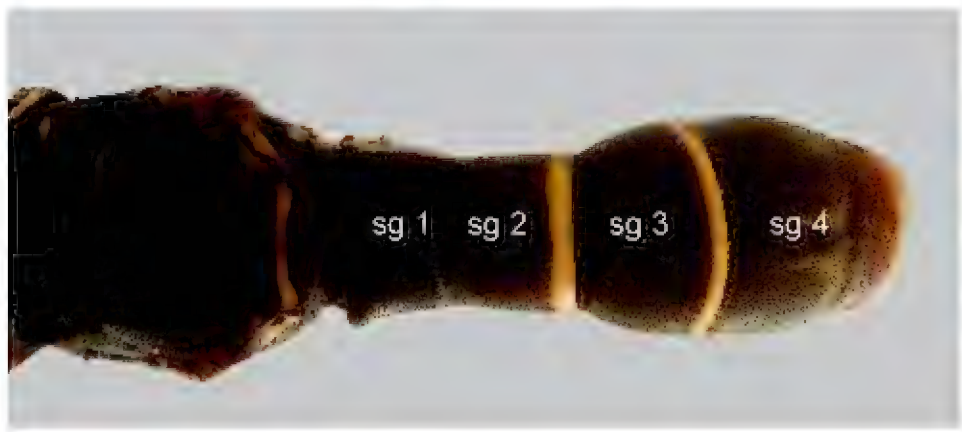
***Paragus* Latreille** (Syrphinae: Paragini)**.** A virtually cosmopolitan genus of *ca* 90 described species, absent from New Zealand, the Neotropical Region south of Costa Rica and Antarctica. Five subgenera are recognised (Vujić *et al*. 2008). The subgenus *P.* (*Afroparagus* Vujić & Radenković) is endemic to the Afrotropics, with two species, the widespread *P. borbonicus* Macquart, 1842 (Fig. 84) and *P. caligneus* Ssymank & Mengual, 2014, described from Gabon and recorded from Central African Republic. The subgenus *Paragus sensu stricto* is mainly restricted to the northern temperate zones, with two species reported from the Arabian Peninsula: *P. binominalis* Smit & Gutiérez-Chacón, 2008 from Yemen and *P. compeditus* Wiedemann, 1830, from Oman and United Arab Emirates (Smit *et al*. 2017). The subgenus *P.* (*Pandasyophthalmus* Stuckenberg) has its greatest diversity in the Afrotropics with 21 species. The subgenus *P.* (*Serratoparagus* Vujić & Radenković) is represented by three (perhaps four) species in the Afrotropics and four species in the Oriental Region, with one species extending into Turkey and another into Australia. *Paragus* (Fig. 84) are small-sized (length: 4–7.5 mm) flies, with a slender, sometimes petiolate abdomen, which is black or black with white or red fasciae and abdominal tergite 1 well-developed (Fig. 206). They occur in xeric to mesic open habitats, such as grasslands or rocky areas, but some species also occur in forests or at forest margins. *Paragus borbonicus* especially is widespread in paddy fields on herbaceous vegetation. Adults



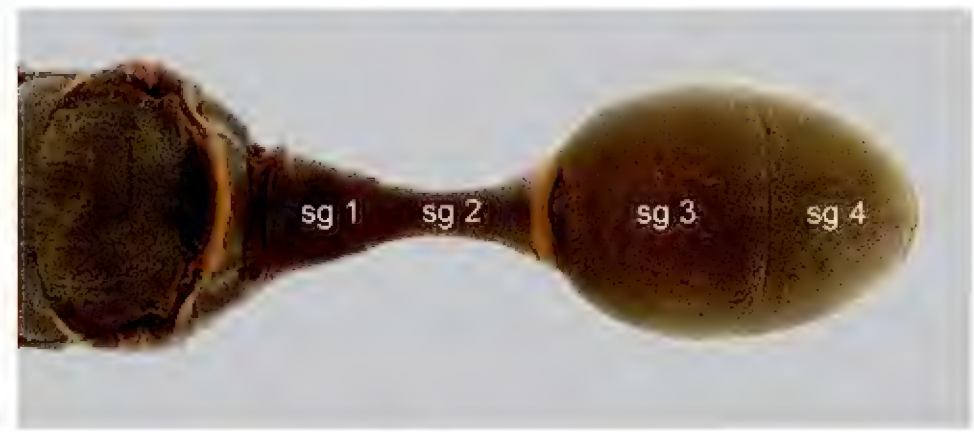
198 *Phytomia*



199 *Asarkina* (*Asarkina*)



200 *Ceriana*



201 *Monoceromyia*

Figs 60.198–201. Abdomens of Syrphidae (dorsal views): (198) *Phytomia* sp.; (199) *Asarkina* (*Asarkina*) sp.; (200) *Ceriana* sp.; (201) *Monoceromyia* sp.

Abbreviations: sg – segment; sct – scutellum.

visit a wide variety of flowers, mostly those in the herb layer and are encountered on Asteraceae with small flower heads (e.g., *Bidens pilosa*, *Emilia*, *Galinsoga* and *Helichrysum*), but also on Commelinaceae, Apiaceae (e.g., *Alepidia*), Malvaceae (e.g., *Sida acuta*) and on other botanical families (Classen *et al*. 2020). Larvae are predatory on Sternorrhyncha. Identification keys for Afrotropical species were provided by Ssymank & Mengual (2014), Stuckenberg (1954*a*, *b*) and Vujić *et al*. (2008).

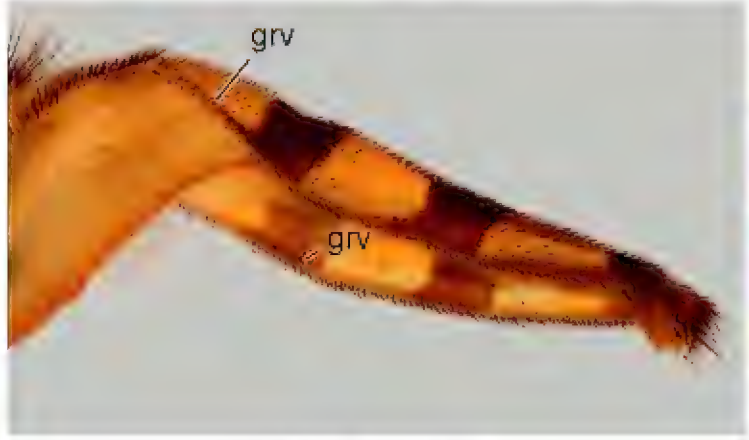
***Paramixogaster* Brunetti** (Microdontinae: Microdontini)**.** An Old World genus of 25 described species occurring in the Afrotropical, Australasian/Oceanian and Oriental Regions. Six species occur in the Afrotropics, including the endemic species *P. elisabethae* (Keiser, 1971) and *P. piptotus* Reemer, 2013 from Madagascar and a recently described species, *P. trifasciatus* Ssymank & Reemer, 2016 with preliminary placement in the genus (Ssymank & Reemer 2016). *Paramixogaster* (Fig. 85) are small- to medium-sized (length: 7–11 mm) flies, with fused abdominal tergites 3 and 4 and wing vein R_{4+5} with a posterior auxiliary vein in cell r_{4+5} (Fig. 162). *Paramixogaster acantholepidis* (Speiser, 1913) and *P. crematogastri* (Speiser, 2013) from South Africa have been reared from ants' nests (subfamilies Formicinae and Myrmicinae) (Speiser 1913), as were a few other extralimital species. Biology and immature stages of Afrotropical species otherwise remain unknown. An identification key to all Afrotropical species is currently unavailable, although the identification key of Curran (1938*a*) to Afrotropical species of *Microdon* incorporates three species currently included in *Paramixogaster*.

***Pelloloma* Vockeroth** (Syrphinae: Syrphini)**.** An endemic genus of three species restricted to high elevations (2,350–3,440 m). *Pelloloma nigrifacies* Vockeroth, 1973 was described from Naude's Nek (South Africa), while *P. winkleri* Kassebeer, 2000 and *P. freidbergi* Kassebeer, 2000 were described from the Ruwenzori range (Uganda) and Mount Kenya (Kenya), respectively. *Pelloloma* (Fig. 86) are small-sized (length: 7–8 mm) robust flies, with an entirely black head and thorax with yellow-orange markings on the abdominal tergites. Biology and immature stages remain unknown. An identification key was provided by Kassebeer (2000*d*).

***Phytomia* Guérin-Méneville** (Eristalinae: Eristalini)**.** A genus of 25 species occurring in the Afrotropical, Oriental and Palaearctic Regions, with 19 species in the Afrotropics, distributed throughout the Afrotropical Region. *Phytomia* (Figs 13, 87) are medium- to large-sized (length: 9–18 mm), robust flies, with very large eyes and a broad head, with a large bare rugose area on the frons dorsal to the antennae (Figs 16, 17). Eyes are holoptic in males (Fig. 16). Some species mimic bees, others are brightly coloured or have patterned wings. Many species possess a "bullae", *i.e.*, a rounded, shiny tubercle in the centre of the abdominal tergites. The genus occurs in a wide range

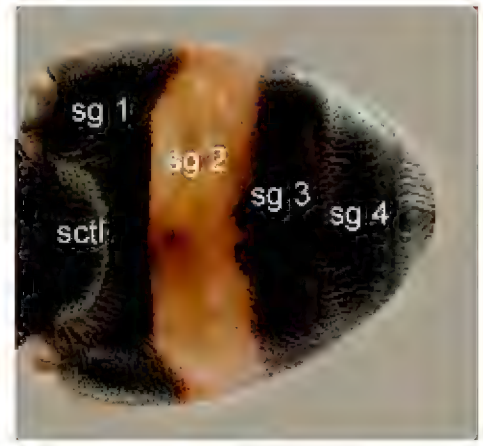
202 *Mesembrius* (*Mesembrius*)

203 *Mesembrius* (*Vadonimyia*)



204 *Asarkina* (*Asarkina*)

205 *Allograpta*



206 *Paragus* (*Afroparagus*)

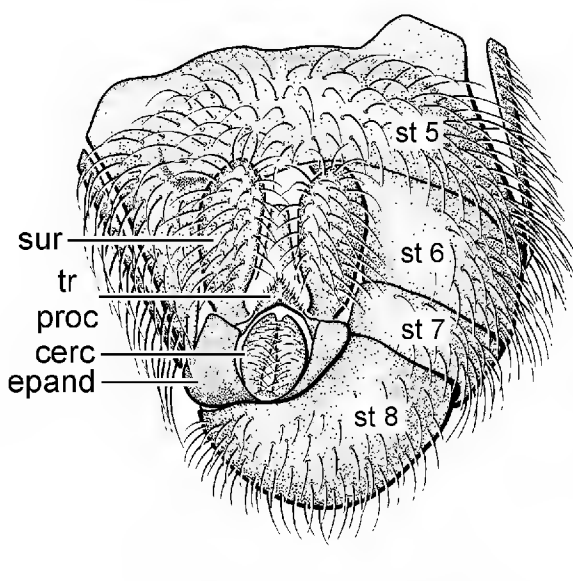
Figs 60.202–206. Abdomens of Syrphidae: (202) *Mesembrius* (*Mesembrius*) sp., lateral view; (203) same, *Mesembrius* (*Vadonimyia*) sp.; (204) same, *Asarkina* (*Asarkina*) sp.; (205) *Allograpta* sp., oblique ventral view; (206) *Paragus* (*Afroparagus*) *borbonicus* Macquart, dorsal view.

Abbreviations: grv – groove; sctl – scutellum; sg – segment.

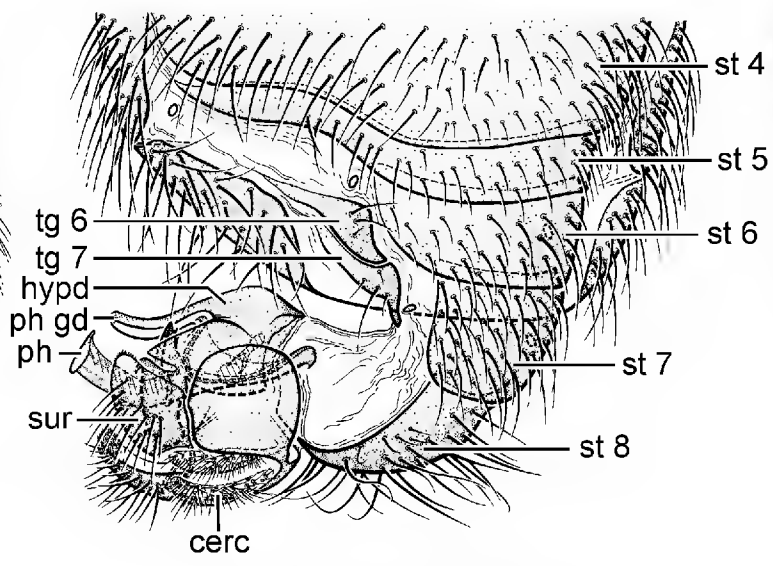
of moist to wet habitat types, such as wetlands, lakes and river valleys, clearings in wet forests, often close to suitable larval habitats, including ditches or eutrophic to highly organic temporary waterbodies. Adults are frequent flower visitors on Asteraceae (e.g., *Bidens*, *Emilia discifolia*, *Euryops* and *Galinsoga parviflora*), but also frequent flowering trees, such as *Nuxia floribunda* Benth. (Stilbaceae) (A. Ssymank & A. Claßen, pers. obs.). Larvae are (semi) aquatic and saprophagous, but the biology and immature stages of Afrotropical species otherwise remain largely unknown. An identification key to 15 Afrotropical species was provided by Curran (1939*b*) (as *Dolichomerus* Macquart and *Phytomia*). An identification key to Afrotropical species was provided by De Meyer *et al*. (2020*a*).

Polybiomyia **Shannon** (Eristalinae: Cerioidini)**.** A genus of 21 described species occurring in the Afrotropical, Australasian, Nearctic and Neotropical Regions. An unknown number of species occur in the Afrotropics, distributed throughout the Afrotropical Region (F.C. Thompson, unpubl.). *Polybiomyia* (Fig. 88) are medium- to large-sized (length: 10–18 mm) wasp-mimics, with a petiolate abdomen, a long antenna with a terminal stylus and wing crossvein *r–m* inserted at or beyond the middle of wing cell *dm* and a moderately sinuose wing vein R_{4+5} (Fig. 165). They can be distinguished from similar genera by the presence of a postmetacoxal bridge (Fig. 113). Adults are attracted to mud pools in the vicinity of slow-moving streams with lush vegetation (G. Goergen & K. Jordaens, pers. obs.). Biology and immature stages of Afrotropical species remain otherwise unknown, but larvae are predatory, developing in decaying plant sap. An identification key to Afrotropical species was provided by Curran (1938*a*) (as *Cerioides*).

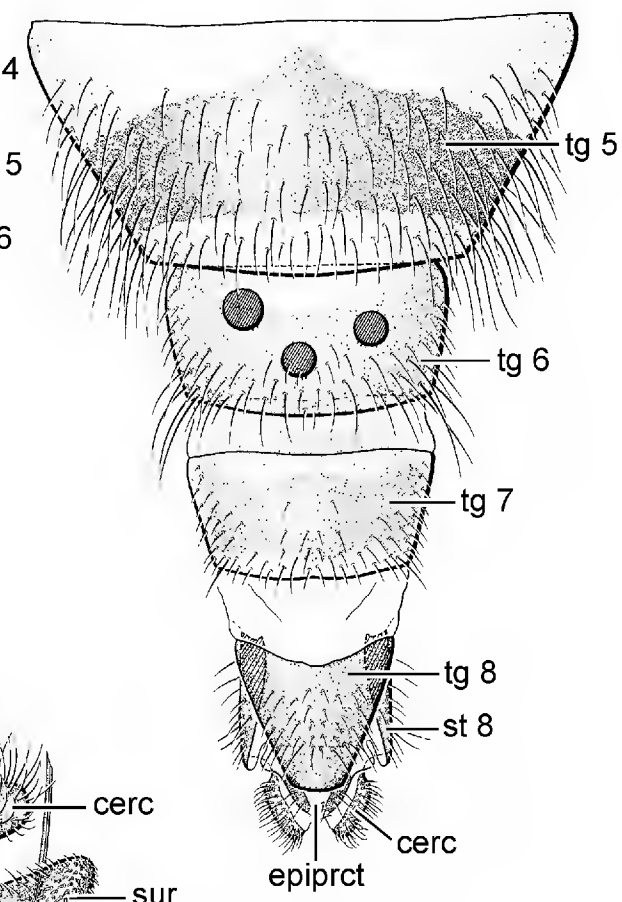
Pseudodoros **Becker** (Syrphinae: Syrphini)**.** A genus of three described species occurring in the Afrotropical, Nearctic,



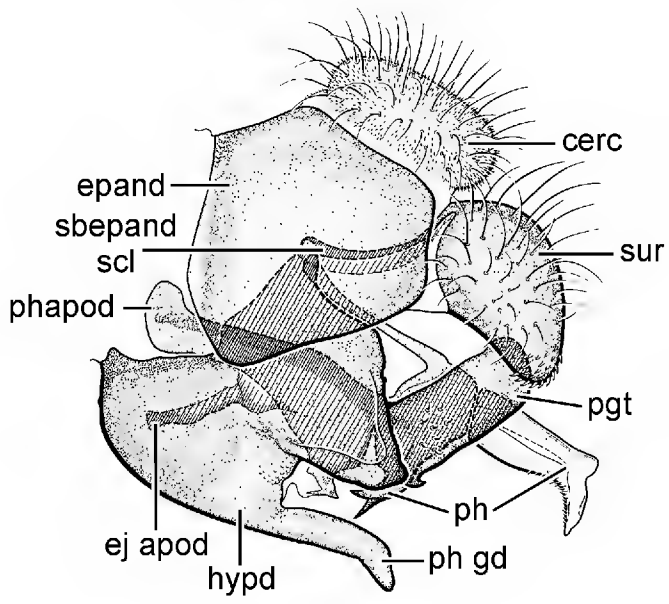
207 *Toxomerus* ♂



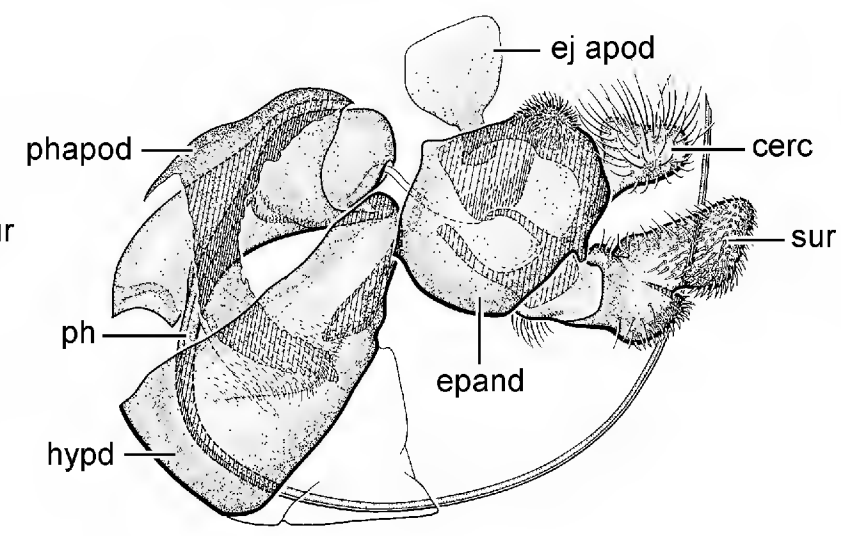
208 *Syrphus* ♂



211 *Syrphus* ♀



209 *Syrphus* ♂



210 *Microdon* (*Microdon*) ♂

Figs 60.207–211. Male and female terminalia of Syrphidae (all non-Afrotropical): (207) male terminalia of *Toxomerus geminatus* (Say), ventral view; (208) same, *Syrphus ribesii* (L.), lateral view; (209) same, lateral view; (210) same, *Microdon* (*Microdon*) *manitobensis* Curran, lateral view; (211) female terminalia of *S. ribesii*, dorsal view. Figs 207–211 (after Vockeroth & Thompson 1987, figs 102–106).

Abbreviations: cerc – cercus; ej apod – ejaculatory apodeme; epand – epandrium; epiprct – epiproct; hypd – hypandrium; pgt – postgonite; ph – phallus; ph gd – phallic guide; phapod – phallapodeme; sbepand scl – subepandrial sclerite; st – sternite; sur – surstylus; tg – tergite; tr proc – triangular process.

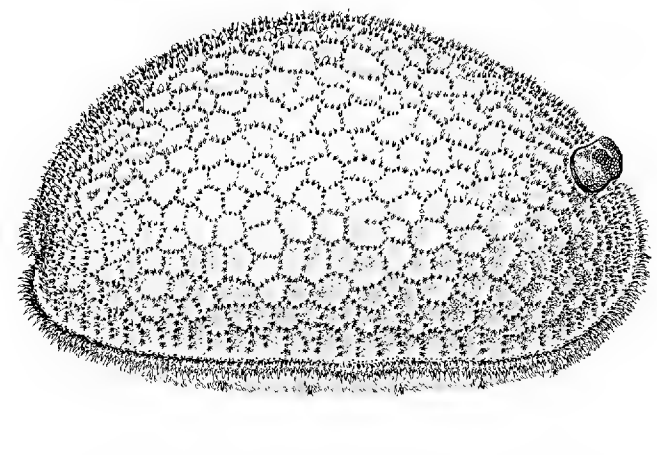
Neotropical and Palaearctic Regions; with the single Afrotropical species, *P. nigircollis* Becker, 1903, occurring in Eastern Africa and Madagascar, the Middle East and Cyprus. Some authors consider the two New World species as the separate genus *Dioprosopa* Hull (Kassebeer 2000*b*). *Pseudodoros* (Fig. 89) are medium-sized (length: 9–12 mm), slender flies, with a petiolate abdomen and a bare laterotergite and anterior anepisternum. Larvae are predatory on Sternorrhyncha. Biology and immature stages otherwise remain unknown.

***Ptilobactrum* Bezzi** (Microdontinae: Microdontini)**.** An endemic monotypic genus, with the single described species, *P. neavei* Bezzi, 1915 (Fig. 90), described from Kenya and further recorded from Uganda. The species is a medium-sized (length: *ca* 13 mm), orange-brown fly, with a broad head and an elongate antennal postpedicel which, in the male, is clothed in long, dense setulae (Fig. 25). *Ptilobactrum* occur in lowland tropical rainforests and larvae probably occur in ants' nests, as is the case with other Microdontinae. Biology and larval morphology otherwise remain unknown.

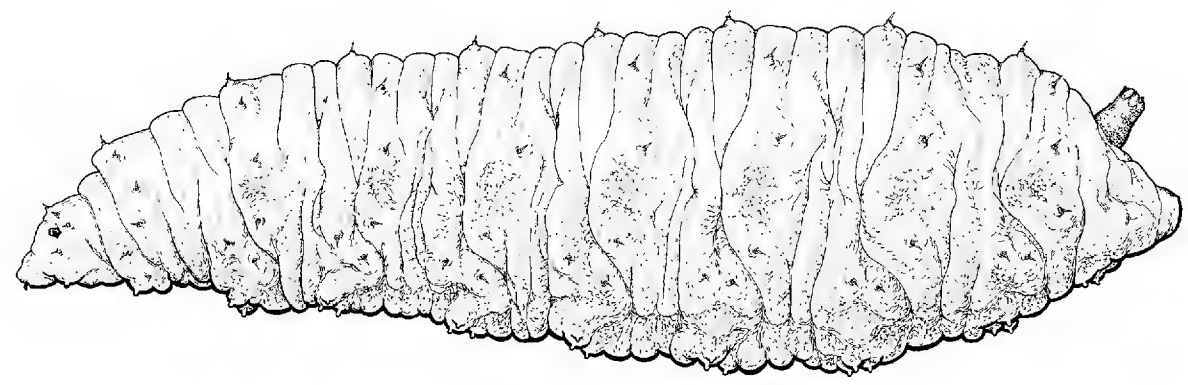
***Rhingia* Scopoli** (Eristalinae: Rhingiini)**.** A genus of 37 species, occurring in all zoogeographical regions, except the Australasian Region and Antarctica. Sixteen species occur in the Afrotropics, distributed throughout the region. *Rhingia* (Fig. 91) are small- to medium-sized (length: 8–11.5 mm) flies, with a broad, brownish to reddish, black or green to bluish metallic abdomen. The face lacks a callus, but they possess a long, proerect "snout", with a long proboscis, sometimes reaching body length (Fig. 91). They are thus able to exploit flowers with deep corollas. One species, *R. cuthbertsoni* Curran, 1939, in which the male eyes are dichoptic, is placed in the endemic monotypic subgenus *R.* (*Eorhingia* Hull). *Rhingia* occur in humid or wet habitats, mostly cloud, rain and riverine forests, with lush herbaceous vegetation. Adults have been sampled on flowers of *Impatiens* (Balsamiaceae), *Isoglossa laxa* Oliver (Acanthaceae), *Pentas lanceolata* (Forssk.) Deflers (Rubiaceae), *Plectranthus* and several Asteraceae, e.g., *Vernonia*, especially early in the morning or in late afternoon until complete darkness (A. Ssymank & K. Jordaens, pers. obs.). Larvae of Palaearctic species are saprophagous in animal dung. Biology and larval morphology of Afrotropical species otherwise remain unknown. An identification key to 13 Afrotropical species was provided by Curran (1939a). A revision of the genus, including an identification key is currently in preparation by Jordaens *et al.* (unpubl.).

***Scaeva* F.** (Syrphinae: Syrphini)**.** A Holarctic genus of 13 species, that extends along the Andes to Chile (five species), two Oriental species and one Palaearctic species, *S. albomaculata* (Macquart, 1842), which is recorded from Cabo Verde (Barkemeyer 2002; Claussen & Barkemeyer 1987) and from United Arab Emirates and Yemen (Smit *et al.* 2017) in the Afrotropical Region. *Scaeva* are medium- to large-sized (length: 10–15 mm) flies, with yellow lateral vittae on the scutum, an inflated frons and densely setulose eyes. Adults are partially migratory and can occur in a variety of habitats. Adults visit flowers of a wide range of plant species, such as Apiaceae, Asteraceae and Euphorbiaceae (A. Ssymank, pers. obs.). Larvae are predatory on Sternorrhyncha.

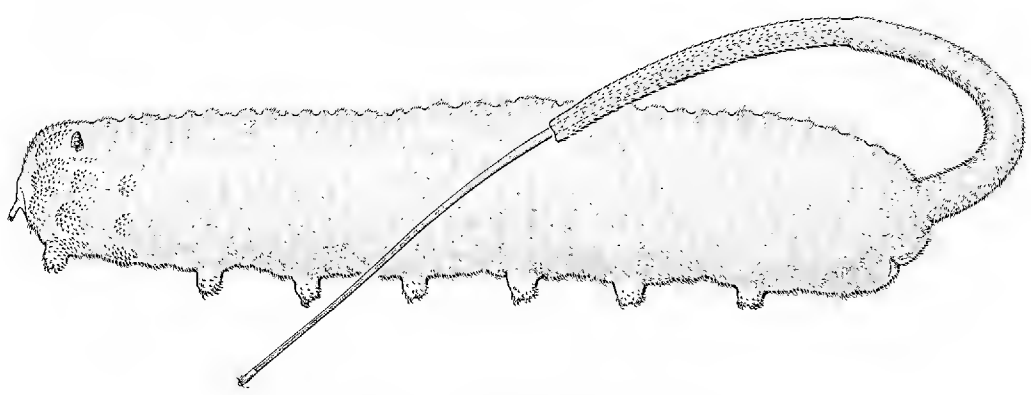
***Senaspis* Macquart** (Eristalinae: Eristalini)**.** An endemic genus of ten species, distributed throughout the Afrotropical Region. The taxonomic position of *S. pennata* is unclear, with the enlarged hind femur and long pilosity on the hind legs. A generic revision, including related genera is required. *Senaspis*



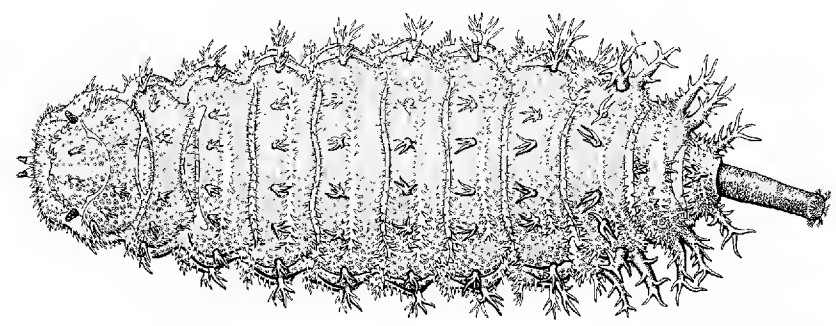
212 *Microdon* (*Microdon*)



214 *Syrphus*



213 *Eristalis* (*Eristalis*)



215 *Brachyopa*

Figs 60.212–215. Larvae of Syrphidae: (212) *Microdon* (*Microdon*) *ruficrus* Williston, dorsolateral view (non-Afrotropical); (213) *Eristalis* (*Eristalis*) *tenax* (L.), lateral view; (214) *Syrphus knabi* Shannon, lateral view (non-Afrotropical); (215) same, *Brachyopa* sp. (non-Afrotropical). Figs 212–215 (after Vockeroth & Thompson 1987, figs 107, 111, 113, 115).

(Fig. 92) are medium- to large-sized (length: 11–21 mm) dark flies, with bare and often maculate eyes and a bare arista (Fig. 40). Wing vein R_{4+5} is strongly sinuate and the membrane is microtrichose, at least in the apical half (Fig. 169). The genus occurs on riverbanks, especially where cattle or other large mammals drink, and near eutrophic to polytrophic standing waterbodies, wetlands and gallery forests along rivers. Data on flower visiting are rare, but they are recorded on cultivated Mango trees, *Mangifera indica*. Larvae are aquatic detritophages, e.g., in polytrophic water (Copeland *et al*. 1999) and sewage ponds and *S. haemorrhoa* has been recorded emerging from pig slurry. An identification key was provided by Curran (1939*b*). An identification key to Afrotropical species was provided by De Meyer *et al*. (2020*b*).

Simoides **Loew** (Eristalinae: Eristalini)**.** An endemic genus of six described species and two undescribed species. *Simoides crassipes* (F., 1805) is distributed throughout the Afrotropics, but the other species have more restricted distributions in South Africa, or in East or West African mountain ranges. *Simoides* include two species-groups, the *S. crassipes*-group, with a long feathery antennal arista and an elongated conical abdomen, and the *S. notatus*-group, with a short-pubescent antennal arista and a more compact abdomen. *Simoides* (Fig. 93) are medium- to large-sized (length: 10–16.5 mm) bee-mimics, with bare eyes, a setulose antennal arista (Figs 18, 19), a wing with a strongly sinuate wing vein R_{4+5} (Fig. 170) and a posterior thoracic spiracle with long setulae on the posterodorsal margin. Male eyes are dichoptic. *Simoides* is closely related to the genus *Phytomia*. Adults occur in a variety of open habitat types, including grasslands, Fynbos, scrub vegetation and along forest margins, mostly in mountainous areas. Adults occur on flowers of many Asteraceae (e.g., *Chrysanthemum*, *Euryops* and *Senecio*), but *S. crassipes* has also been recorded from flowers of a wide range of cultivated or medical plants, e.g., *Hoslundia opposita* Vahl (Lamiaceae), *Lantana camara* L. (Verbenaceae), *Persea americana* (Lauraceae) and *Sesamum angustifolium* (Oliv.) Engl. (Pedaliaceae) (A. Ssymank, pers. obs.). Larval biology and immature stages remain unknown. An identification key to two species was provided by Curran (1939*b*). A revision of the genus with an identification key is currently in preparation by Ssymank *et al*. (unpubl.).

Sphaerophoria **Le Peletier & Serville** (Syrphinae: Syrphini)**.** A predominantly northern temperate genus of *ca* 80 species, with a limited distribution into the south temperate areas of the Afrotropical and Australasian Regions. Four species occur in the Afrotropics. *Sphaerophoria* (Fig. 94) are small- to medium-sized (length: 8–11 mm) slender flies, with yellow lateral vittae on the scutum, which do not extend beyond the transverse suture in Afrotropical species. They have a black abdomen with, in some species, yellow fasciae. *Sphaerophoria* occur in open habitats and scrubland, including ruderal areas. Larvae are predators of Sternorrhyncha and larvae of *S. quadrituberculata* Bezzi, 1915 have been reported to feed on Thysanoptera (Dirickx 1998: 128). An identification key was provided by Vockeroth (1973).

Spheginobaccha **de Meijere** (Microdontinae: Spheginobacchini)**.** An Old World tropical genus of 18 species; eight in the Afrotropical Region and ten species in the Oriental Region. Afrotropical species are recorded from Malawi, South Africa and Madagascar. *Spheginobaccha* (Fig. 95) are medium- to large-sized (length: 13–16 mm) flies, with a long, elongated abdomen, an evenly rounded oral margin (Fig. 20) and a complete transverse suture to the thorax. Immature stages of the genus are possibly associated with ants' nests, in view of the supposed sister-group relationship with other Microdontinae, which all develop in such nests. Biology and immature stages otherwise remain unknown. An identification key to Afrotropical species was provided by Thompson & Hauser (2015).

Sphiximorpha **Rondani** (Eristalinae: Cerioidini)**.** A widely distributed genus of 55 described species, occurring in all zoogeographical regions, but absent from New Zealand and Antarctica. Ten species are recorded from the Afrotropics, distributed throughout the region. *Sphiximorpha* (Fig. 96) are medium-sized (length: 9–10 mm) wasp-mimics, with long, proerect antennae with a terminal stylus, but without or only a very short, frontal prominence (Fig. 22). The wing crossvein *r–m* is positioned at or beyond the middle of wing cell *dm* and has a moderately sinuose vein R_{4+5} (Fig. 173). Larvae are saprophagous in wet decaying wood and decaying plant sap. Adults are attracted to mud pools in the vicinity of slow-moving streams with lush vegetation (G. Goergen & K. Jordaens, pers. obs.). Biology and larval morphology of Afrotropical species remain otherwise unknown. An identification key to Afrotropical species was provided by Curran (1938*a*) (as *Cerioides*).

Syritta **Le Peletier & Serville** (Eristalinae: Milesiini)**.** A genus of *ca* 60 species occurring in the Afrotropical, Australasian/Oceanian, Oriental and Palaearctic Regions. Two common species, *S. flaviventris* Macquart, 1842 and *S. pipiens* (L., 1758), were introduced into the Nearctic and Neotropical Regions. *Syritta* has the greatest diversity in the Afrotropics with 42 species distributed throughout the region. Of the 16 species-groups recognised by Lyneborg & Barkemeyer (2005: 22), 13 are represented in the Afrotropics. The Australasian and Oriental Regions have 15 species and six occur in the Palaearctic. *Syritta* (Fig. 97) are small- to medium-sized (length: 5–9 mm) flies, with a slender abdomen and legs with a greatly enlarged hind femur, with an anteroventral spinose carina in the apical third. In a number of Afrotropical species the spurious wing vein is reduced or absent. *Syritta* inhabit a wide variety of habitats, with some species-groups restricted to subtropical or cloud forests and their margins at high elevations, while other species have been recorded from xeric, open habitats, such as rocky outcrops, dry grasslands, savanna or semi-deserts. They are also widespread in other open habitat types, including wetlands and ruderal sites, crop fields and gardens. Adults have been found on flowers of a variety of herb species, such as Asteraceae (e.g., *Emilia*, *Euryops* and *Helichrysum*), shrubs (e.g., *Rhus* (Anacardiaceae) and *Rubus*) and trees (e.g., *Phyllanthus discoideus*), including cultivated plants (*Mangifera indica* and *Fragaria* x *ananassa* Duchesne, strawberry cultures (Rosaceae)) (Classen *et al*. 2020). Larvae are saprophagous in decaying organic material. An identification key to Afrotropical species was provided by Lyneborg & Barkemeyer (2005: 27), with one additional described species and key adaptation by Steenis (2010).

Syrittosyrphus **Hull** (Eristalinae: Milesiini)**.** An endemic monotypic genus, with the single described species, *S. opacea* Hull, 1944, described from Somerset East in South Africa. *Syrittosyphus opacea* (Fig. 98) is a large-sized (length: 14–15 mm) brownish fly, with an elongated abdomen. The apical margin of the scutellum has a characteristic flattened rim (Fig. 105) and males have two long spines on the hind coxa (Fig. 184).

The species occurs in Afromontane forests in mountain ranges of Southern and East Africa, with *Ocotea* (Lauraceae), *Podocarpus* (Podocarpaceae) and *Xymalos* (Monimiaceae). Adults rest on leaves or alight on the ground in forests. Biology and immature stages remain unknown. A description of the female was provided by Ssymank & Jordaens (2021).

***Toxomerus* Macquart** (Syrphinae: Toxomerini)**.** A genus of *ca* 150 species largely confined to the Neotropical Region, but also occurring in the Nearctic Region. One species, *T. floralis* (F., 1798), was recently introduced into the Afrotropics (Jordaens *et al*. 2015), where it is now rapidly dispersing and becoming established in tropical areas. *Toxomerus floralis* (Figs 99, 176) is a small- to medium-sized (length: 6–9 mm) slender species, with yellow lateral vittae on the mesonotum, extending from the postpronotum to the scutellum and a distinct triangular emargination at the posterior margin of the eye (Fig. 38), not present in other Afrotropical syrphids. The species is found in

Figs 60.216–223. Immature stages of Syrphidae: (216) larval habitus of Microdontinae species, dorsal view; (217) same, *Toxomerus floralis* (F.); (218) same, *Eristalinus* (*Eristalodes*) sp., dorsal view; (219) puparial habitus of *T. floralis*, lateral view; (220) larval habitus of *Merodon* sp., dorsolateral view; (221) same, *Eumerus* sp., lateral view; (222) same *Graptomyza* sp., dorsal view; (223) puparial habitus of *Polybiomyia* sp., dorsal view. Fig. 216 (photograph © S.A. Marshall), Figs 217, 219, 223 (photographs © G. Goergen), Fig. 222 (photograph © A. Aracil), Figs 220, 221 (photographs © E. Rättel), Fig. 218 (photograph © M. Inés Lillo).

anthropogenic habitats, such as gardens, plant nurseries and agricultural fields. Adults visit flowers of grasses and sedges and can be very abundant. Larvae (Fig. 217) have been found feeding on pollen of *Cyperus rotundus* L. (Cyperaceae) and *Mitracarpus hirtus* L. DC. (Rubiaceae) (Jordaens *et al*. 2015).

***Tropidia* Meigen** (Eristalinae: Milesiini)**.** A genus of *ca* 16 species occurring in the Afrotropical, Australasian/Oceanian, Nearctic, Neotropical and Palaearctic Regions. Four species occur in the Afrotropics, distributed in Cameroon, Democratic Republic of Congo, Nigeria and Madagascar. *Tropidia* (Figs 100, 177) are small- to medium-sized (length: 7–11 mm) flies, with a characteristic spur on the hind femur (Fig. 193). Larvae probably develop in decaying plant material in wet areas, but the biology and immature stages of Afrotropical species remain unknown. Unpublished molecular work suggests that the genus *Tropidia* does not occur in the Afrotropics and that all Afrotropical *Tropidia* should be included in *Calcaretropidia* (Moran *et al*. unpubl.). An identification key to Afrotropical species was provided by Keiser (1971).

***Xanthandrus* Verrall** (Syrphinae: Bacchini)**.** A virtually cosmopolitan genus of 28 species, occurring in all zoogeographical regions, except Antarctica, but absent from New Zealand. Three species occur in the Afrotropics, ascribed to the endemic subgenus *X.* (*Afroxanthandrus* Kassebeer), namely: *X.* (*A.*) *congensis* (Curran, 1938) and *X.* (*A.*) *longipilus* Kassebeer, 2000, both described from Democratic Republic of Congo and *X.* (*A.*) *magnificus* Thompson, 2019, described from São Tomé and Príncipe (Goeldlin de Tiefenau & Thompson 2019). *Xanthandrus* (Fig. 101) are medium-sized (length: 10–13 mm) flies, with a black face and scutellum and a specific setulae pattern on the katepisternum. Larvae are predators of caterpillars, but the biology and immature stages of Afrotropical species remain unknown. An identification key to Afrotropical species was provided by Kassebeer (2000*c*) and Goeldlin de Tiefenau & Thompson (2019).

***Xylota* Meigen** (Eristalinae: Milesiini)**.** A genus of more than 100 species, occurring in all zoogeographical regions, except Antarctica, with greatest diversity in the northern temperate zones. The ten Afrotropical species are ascribed to the endemic subgenus *X.* (*Hovaxylota* Keiser) and are distributed in Central and East Africa and in Madagascar. *Xylota* (Fig. 102) are medium-sized (length: 10–13 mm) flies, with a slender abdomen and hind femora with spines, but without expansions or carinae (Fig. 194). Adults occur in, or in close proximity to, forests, some species are flower visitors and others imbibe pollen from leaf surfaces. Larvae are saprophagous in wet decaying tree sap and wood. Biology and larval morphology of Afrotropical species remain unknown. An identification key was provided by Hippa (1985*a*).

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PIPUNCULIDAE 61

(Big-headed Flies)

Marc De Meyer, Mihály Földvári and Jeffrey H. Skevington

Fig. 61.1. Female of *Cephalops* sp. (non-Afrotropical) (photograph © S.A. Marshall).

Diagnosis

Small-sized (body length: 2.0–11.5 mm), usually uniformly dark brown to black coloured flies (Fig. 1) (a few species predominantly yellow); easily recognised by the semi-globose to globose head, that is largely occupied by the compound eyes (Figs 2–4), the long and rather narrow wings (Figs 19–26), and in the female, the piercing ovipositor, adapted for injecting eggs into the host (Fig. 28).

Head semi-globose, with narrow occiput in Chalarinae (Fig. 2) or globose with broadened occiput in Nephrocerinae and Pipunculinae (Figs 3, 4); compound eye occupying most of head, female with enlarged anterior ommatidia (indistinct in non-Afrotropical *Nephrocerus* Zetterstedt), male eyes usually contiguous on frons for varying distance, except for Chalarinae and some Tomosvaryellini; ocellar setae present in Chalarinae (Fig. 2), lacking in other pipunculids (Figs 3, 4); frons with varying degree of pruinescence; antennal postpedicel obtuse to filiform in shape, with dorsal arista (Fig. 7).

Thorax generally with dark brown to black ground colour, with varying degrees of greyish or brownish pruinescence, rarely yellow or shiny metallic blue or black; proepisternum sometimes bearing fan-like setal tuft (Fig. 10). Wing (Figs 19–26) in comparison to body length rather long and narrow, membrane usually hyaline, rarely fumose (as in *Claraeola congopennis* (Hardy, 1949)), iridescent in direct light; pterostigma present or absent; cell r_{4+5} open (Figs 19–26). Legs (Figs 12–18) usually simple, occasionally with conspicuous spines or appendages on trochanter or femur; tarsal claws and pulvilli larger in female than male.

Abdomen (Figs 27–34) sub-cylindrical, colouration and pruinescence similar to thorax, occasionally more pronounced greyish pruinescence or with yellow markings; tergite 1 usually with row of setae or setal tuft laterally (Figs 30–33); male

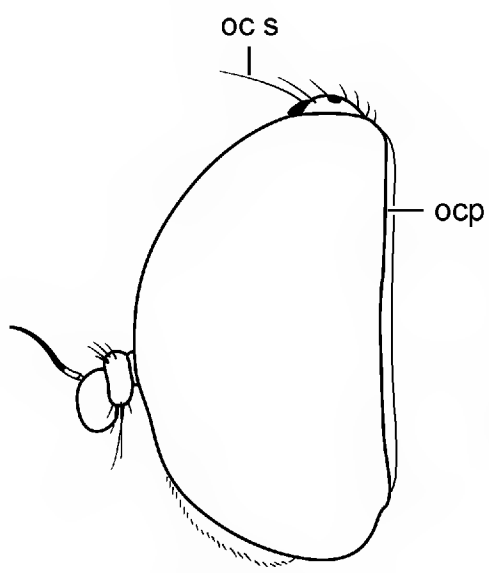
Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2021. Manual of Afrotropical Diptera. Volume 3. Brachycera—Cyclorrhapha, excluding Calyptratae. *Suricata* 8. South African National Biodiversity Institute, Pretoria; pp. 1493–1505.

terminalia (Figs 27, 29, 35–41) with segments 6 and 7 asymmetrically developed and twisted left (Fig. 27); tergites 6 and 7 usually strongly reduced (Fig. 29), except in Chalarinae, in which they are present and distinct (Fig. 30); male syntergosternite 8 large, forming tip of abdomen, apically with (Fig. 35) or without (Fig. 36) membranous area; surstyli symmetrical (Fig. 35) to strongly asymmetrical (Fig. 36), rather simple to highly modified; female terminalia modified into piercing ovipositor (Fig. 28); in Chalarinae and Pipunculinae ovipositor originates from abdominal segments 7, 8 and 9.

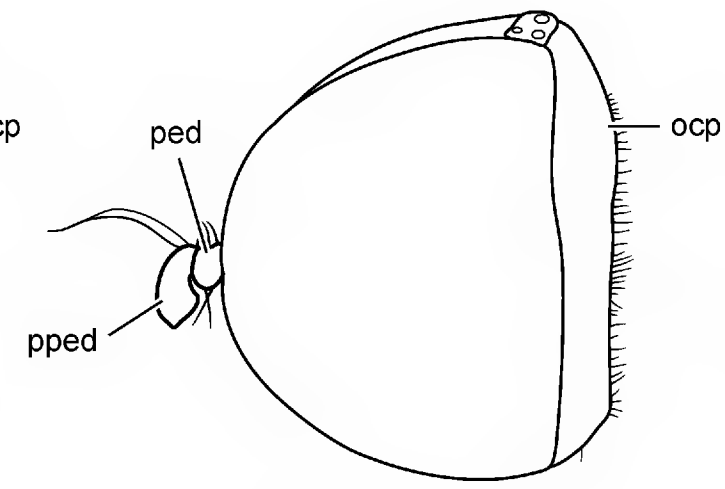
No eggs of Afrotropical pipunculids have been studied. The description here is based on Kozánek *et al*. (1998: 143). Egg distinctly elongate, broadly rounded at one end, remaining equally broad for *ca* ½ length, gradually narrowing to end; chorion smooth, transparent; egg swells and becomes rounded during development (Jervis 1980).

No larvae of Afrotropical pipunculids have been studied. The description here is based on Kozánek *et al*. (1998: 143). Larva cylindrical, tapering at both ends, slightly more pointed anteriorly; body with pseudocephalon, caudal vesicle and 10 visible body segments; integument wrinkled, with transverse bands of minute spines (first-instar) or fine granules (second-instar), cuticle smooth and transparent; 2 (but presumably 3) larval instars are known during development; first-instar larva with cephaloskeleton weakly sclerotised; spiracles absent; second-instar with well-developed cephaloskeleton (see Fig. 50 from puparium); rudimentary antenna and maxilla present on head; respiratory system amphipneustic; 1 pair of prothoracic spiracles, second pair on heavily sclerotised posterior plate (not in *Nephrocerus*); caudal vesicle bilobed, well-developed in first-instar, less distinct in second-instar. Additional descriptive details for (non-Afrotropical) species can be found in Albrecht (1990), Benton (1975: 83) and Morakote & Yano (1987).

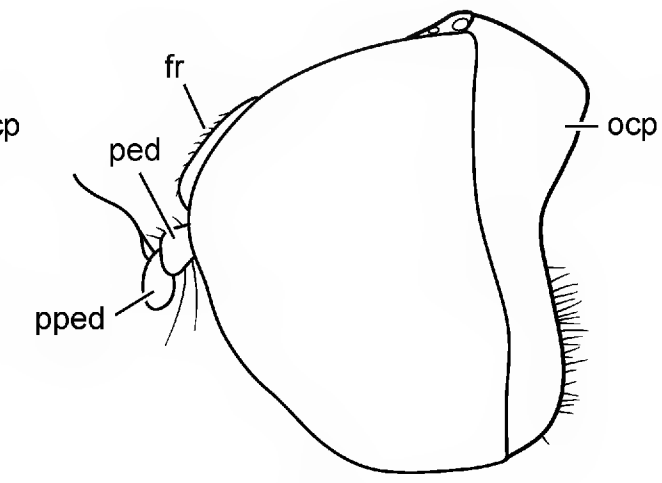
The puparium of only one Afrotropical pipunculid, *Tomosvaryella singula* Hardy, 1950 is known (Kirk-Spriggs 1988). This description is based on Kozánek *et al*. (1998: 143) with additions from Kirk-Spriggs (1988). Puparium (Fig. 47) broadly oblong, squat, rounded at ends; colour reddish to brown (rarely



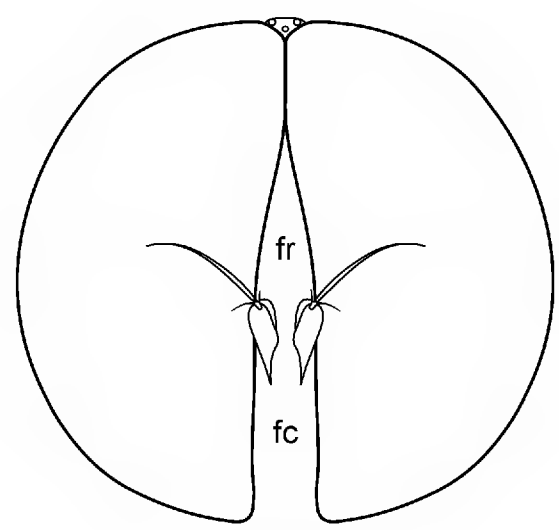
2 *Chalarus*



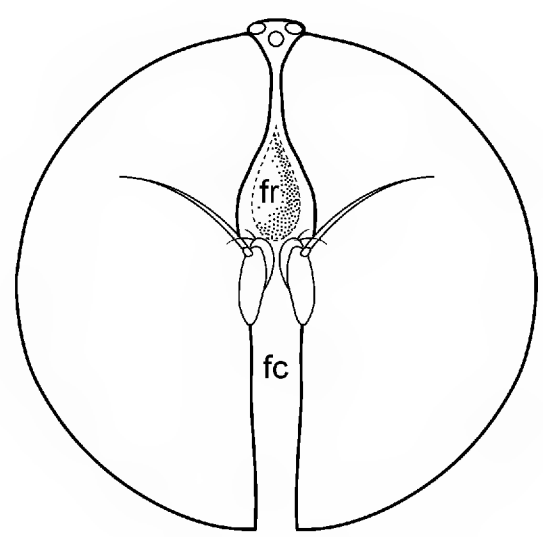
3 *Pipunculus*



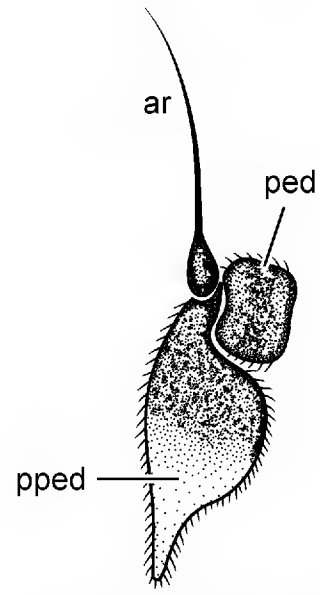
4 *Collinias*



5 *Dasydorylas*



6 *Collinias*



7 *Tomosvaryella*

Figs 61.2–7. Heads and antenna of Pipunculidae: (2) head of *Chalarus* sp., lateral view (non-Afrotropical); (3) same, *Pipunculus hertzogi* (Rapp) (non-Afrotropical); (4) same, *Collinias* sp. (non-Afrotropical); (5) same, *Dasydorylas eucalypti* (Perkins) (non-Afrotropical), anterior view; (6) same, *Collinias* sp. (non-Afrotropical); (7) antenna of *Tomosvaryella singula* Hardy, lateral view. Figs 3–6 (after Skevington & Yeates 2000, figs 2C, 2B, 2G, 2H, respectively), Fig. 7 (after Kirk-Spriggs 1988, fig. 3).

Abbreviations: ar – arista; fc – face; fr – frons; ocp – occiput; oc s – ocellar seta; ped – pedicel; pped – postpedicel.

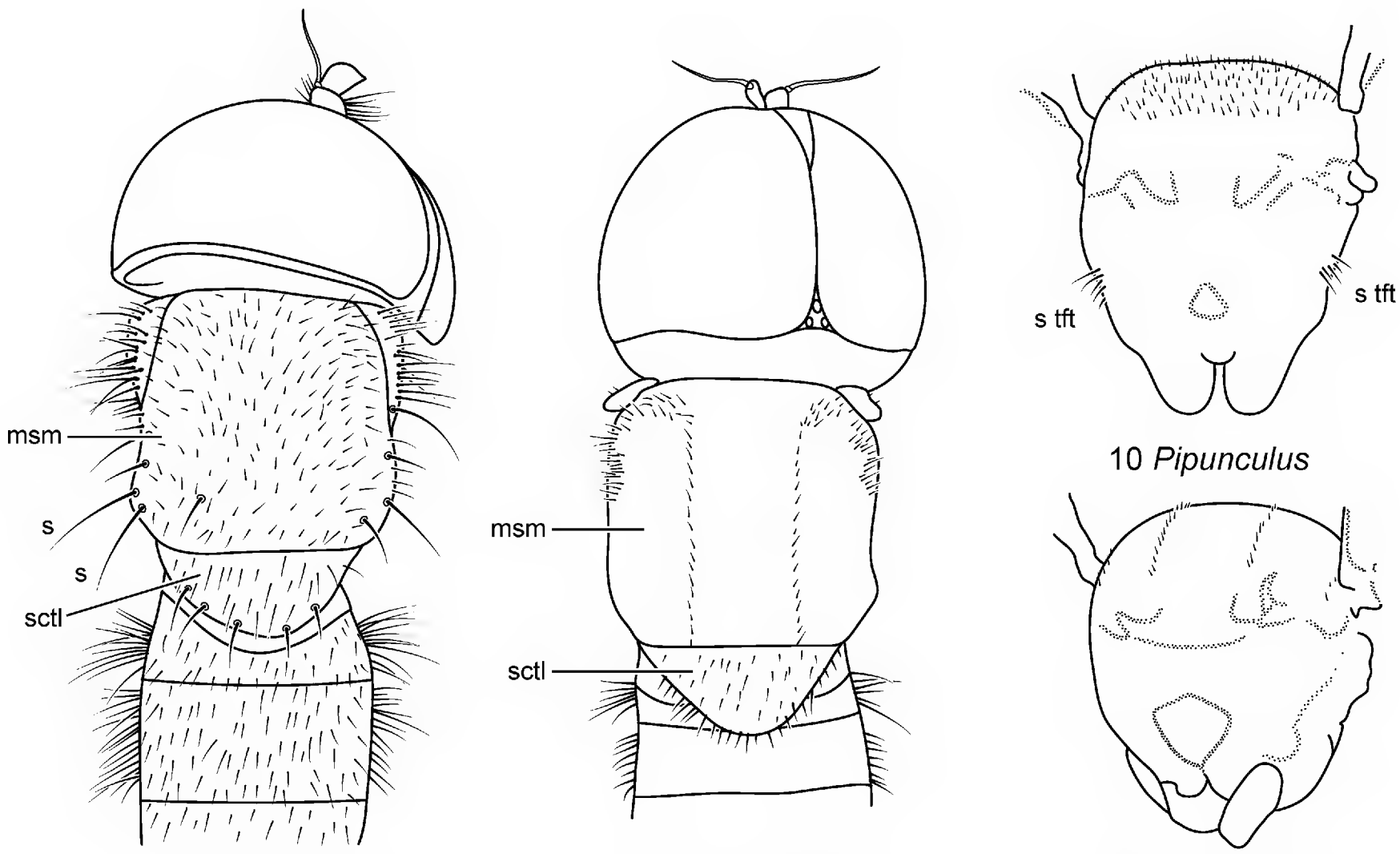
blackish); cuticle rather smooth (creeping welts reduced in *T. singula*), areolate, with areolae more or less deeply embedded in cuticle; papillae on integument arranged in groups, distinct on abdominal segments 2–6, less so towards head and barely discernible at posterior end; abdominal region consists of 5–6 visible segments; prothoracic and posterior spiracles present (Fig. 49), latter on posterior spiracular plate; 2 small, slender prothoracic horn-like spiracles project anterolaterally (respiratory horns *sensu* Kirk-Spriggs 1988) (Fig. 48); spiracular plate in *T. singula* oval in shape, with 3 spiracular openings running along ridges; during eclosion, two main puparial caps at anterior end of puparium detached, one dorsal and one ventral (in *T. singula*, anterior part breaks into 3 puparial caps, see Fig. 47) (Albrecht (1990) revealed five different types of rupturing in recent pipunculids).

Adult Pipunculidae typically resemble dark coloured Syrphidae (see Chapter 60), but can be differentiated from these by the above-mentioned characters and by the lack of a spurious wing vein (in most cases) and the open r_{4+5} wing cell. Some Bombyliidae (see Chapter 45), such as the Palaearctic genus *Lomatia* Meigen and the non-Afrotropical tribe Petrorossiini, superficially resemble pipunculids when encountered in the field, but these lack the dorsal antennal arista found in Pipunculidae.

Biology and immature stages

Most pipunculids that have been studied are endoparasitoids of several Hemiptera (Auchenorrhyncha) families, including: Cercopidae, Cicadellidae (e.g., Figs 45, 46), Cixiidae, Delphacidae, Flatidae, Issidae and Membracidae. The only known exception occurs in the non-Afrotropical genus *Nephrocerus*. These unusual flies attack adult crane flies (Tipulidae) (Kehlmaier & Floren 2009; Koenig & Young 2007). Despite the economic importance of the host groups in agriculture, few data on host relationships exist and some genera have no known hosts (for example, the non-Afrotropical genera *Allomethus* Hardy, *Basileunculus* Rafael, *Elmohardyia* Rafael and *Protonephrocerus* Collin).

Adults are frequently observed hovering among vegetation and their flight is similar to that of Syrphidae. Adults utilise all terrestrial habitats, but diversity and numbers are greatest in forest openings and along forest edges (perhaps due to easier observation). In semi-arid regions, adults commonly occur at seeps or along small creeks. Adult flies feed on honeydew and can occasionally be found in large, mixed feeding groups on Auchenorrhyncha secretions (Skevington & Marshall 1998). Due to this behaviour, they are often attracted to artificial



8 *Jassidophaga* 9 *Dasydorylas* 10 *Pipunculus* 11 *Eudorylas*

Figs 61.8–11. Heads and thoraces and prothoraces of Pipunculidae (all non-Afrotropical): (8) thorax and abdomen of *Jassidophaga* sp., dorsal view (non-Afrotropical); (9) same, *Dasydorylas eucalypti* (Perkins); (10) prothorax of *Pipunculus thomsoni* Becker, anterior view (head removed); (11) same, *Eudorylas zonellus* Collin. Figs 8, 9 (after Skevington & Yeates 2000, figs 3C, 3A, respectively), Figs 10, 11 (after Coe 1966, figs 21, 22).

Abbreviations: msm – mesonotum; s – seta; s tft – setal tuft; sctl – scutellum.

honeydew sprayed on vegetation (a mixture of honey, cola and water). Two Palaearctic species have also been observed feeding on nectar from flowers (Kehlmaier 2015). This requires further confirmation, however, as these flies were likely simply utilising flowers as a perch and it is not certain that actual nectar-feeding took place. Occasionally, mating pairs are discovered hovering *in copula* or temporarily settled on vegetation. Pronounced sexual dimorphism in pipunculids makes association of the sexes difficult, so these occasional discoveries are useful.

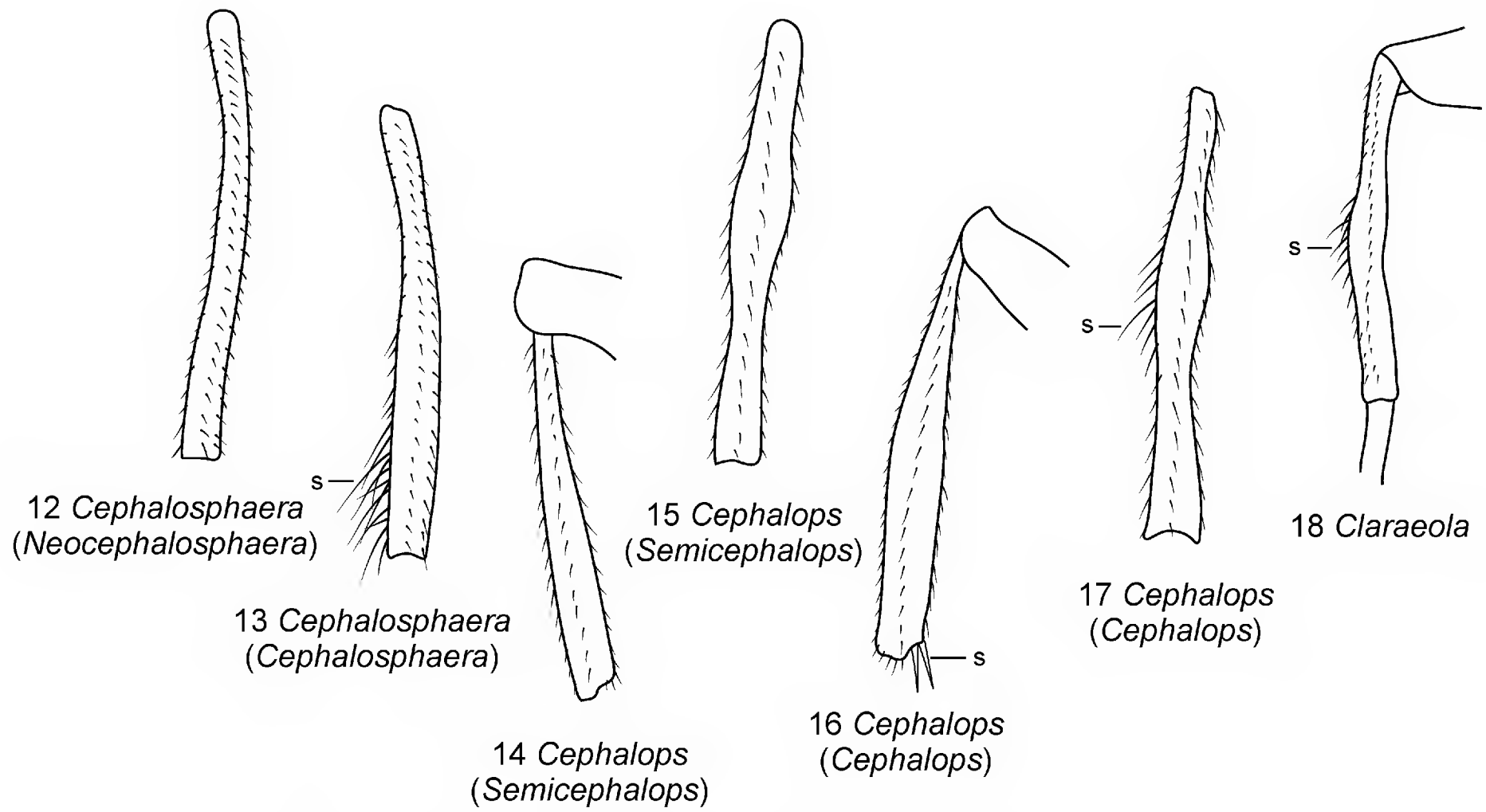
Females of most pipunculid species deposit their eggs in early instar nymphs or adults of their hosts. After visually locating a host, some species remove the host from the food-plant and oviposit one egg inside each host while in flight (Huq 1982: 20; May 1979; Williams 1919), whereas others leave the host *in situ* (Benton 1975: 77). Larvae develop to maturity within the nymph or adult hosts (e.g., Figs 45, 46). When mature, the larva exits the host through a break in one of the dorsal inter-segmental membranes of the abdomen in order to pupariate in the soil, in leaf litter, at the base of plants or rarely, attached to leaves (Ferrar 1987: 291; Perkins 1905). More detailed information on immature stages, together with information on rearing techniques can be found in Belcari (1999), Benton (1975: 3), Coe (1966: 18), Ferrar (1987: 291), Freytag (1988: 519), Huq (1984), Jervis (1980), Morakote & Yano (1987) and Perkins (1906).

Pipunculid/host associations are best known for the European fauna (Waloff & Jervis 1987: 281), followed by the Nearctic Region (Skevington & Marshall 1997) and the Australasian Region (Skevington 2001). For the Afrotropical fauna, only two associations are known between pipunculids and potential hemipteran hosts. Kirk-Spriggs (1988) describes the association of *Tomosvaryella singula* with *Cofana spectra* (Distant) (Cicadellidae), which is an abundant pest in rice fields in Nigeria. He referred to the presence of both and to possible additional parasitism in northern Cameroon (Descamps 1956). De Meyer (1995) reported *Clistoabdominalis nitidifrons* (Becker, 1900) (under the junior synonym *Eudorylas confusoides* (Lamb, 1922)), as a parasitoid of *Cicadulina mbila* (Naudé) (Cicadellidae) in Réunion Is.

Most pipunculid species attack more than one species of host, but show a preference for a particular set of host species. Only two species have been reared from more than one subfamily of host (Skevington 2001). Superparasitism and multiple parasitism are rare and survival of more than one pipunculid in these cases is exceptional (Jervis 1980; Koenig & Young 2007; Morakote & Yano 1988; Waloff & Jervis 1987: 330).

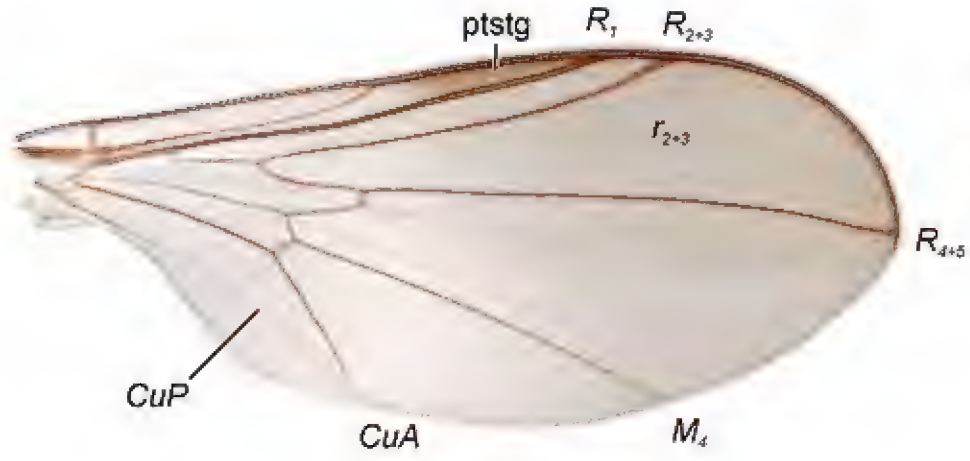
Economic significance

The potential value of Pipunculidae for biological control has stimulated some research on the bionomics of the family. For example, research into the control of the Potato leafhopper,

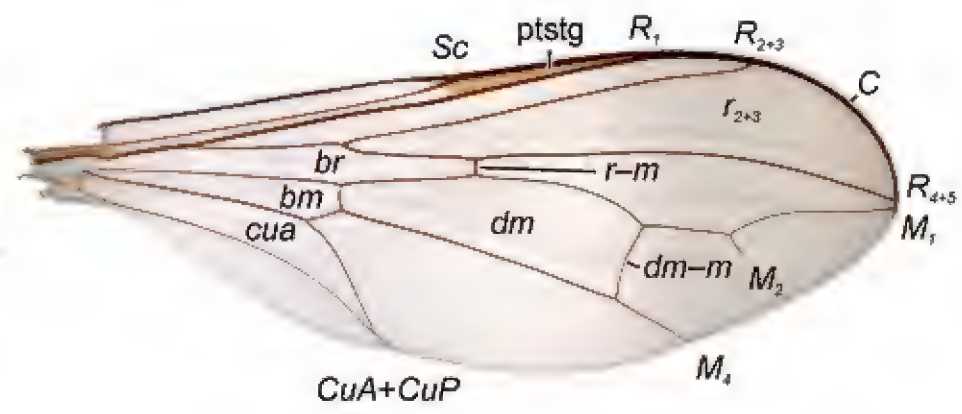


Figs 61.12–18. Legs of Pipunculidae: (12) hind tibia of *Cephalosphaera* (*Neocephalosphaera*) *brevis* (Cresson) (non-Afrotropical), anterodorsal view; (13) same, *Cephalosphaera* (*Cephalosphaera*) *appendiculata* (Cresson) (non-Afrotropical); (14) mid tibia of *Cephalops* (*Semicephalops*) *saegeri* (Hardy), anterior view; (15) same, hind tibia dorsal view; (16) mid tibia of *Cephalops* (*Cephalops*) *candidulus* (Hardy), anterior view; (17) same, hind tibia, dorsal view; (18) hind tibia of *Claraeola* sp., anterodorsal view. Fig. 18 (after Skevington & Yeates 2000, fig. 3G).

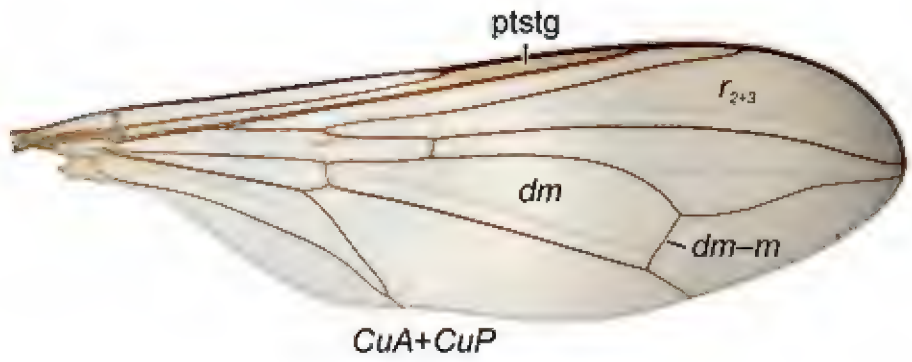
Abbreviation: s – seta.



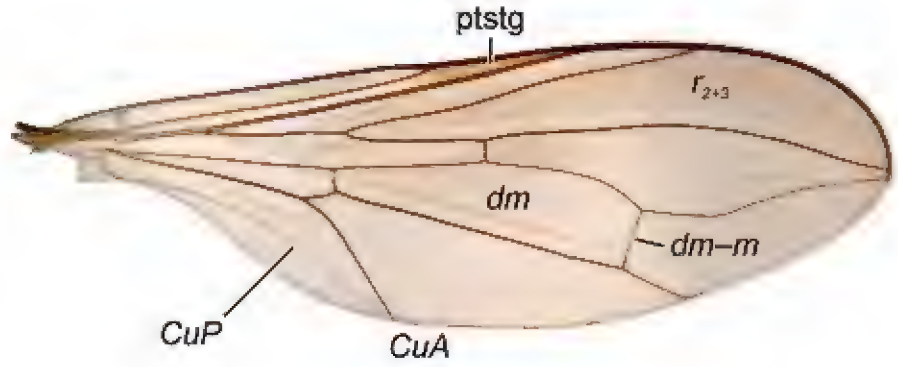
19 *Chalarus*



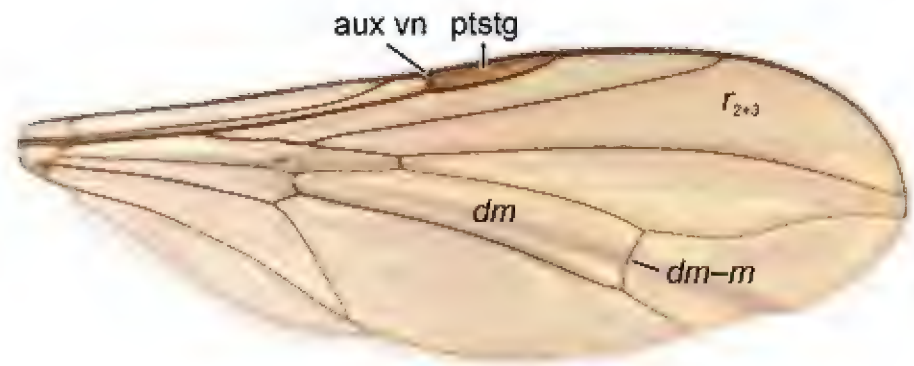
20 *Cephalosphaera*



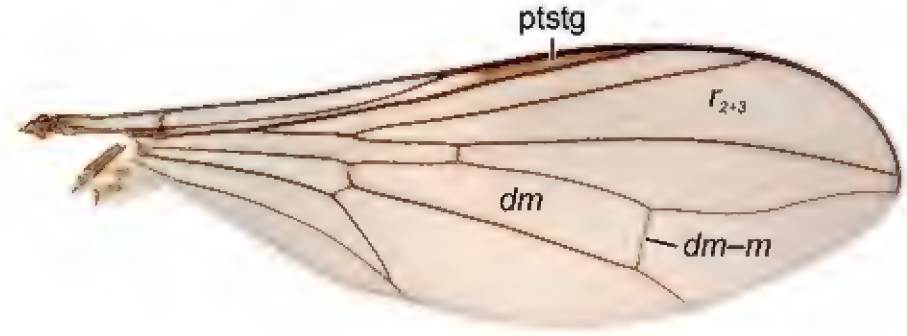
21 *Cephalops*



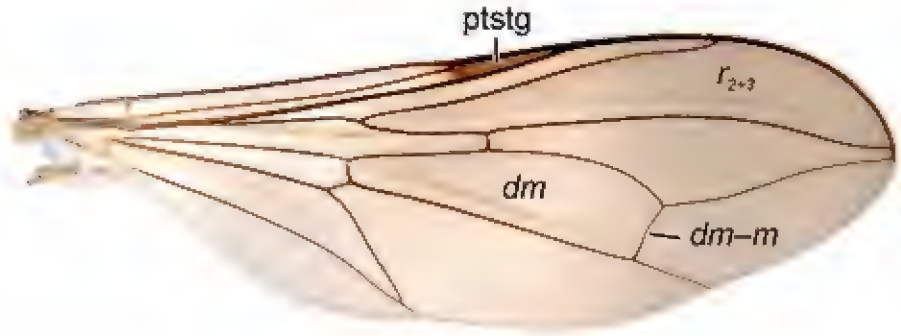
22 *Cephalops* (*Beckerias*)



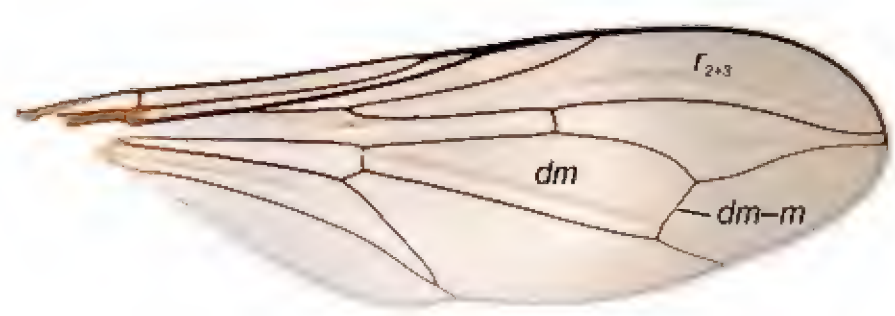
23 *Collinias*



24 *Microcephalops*



25 *Eudorylas*



26 *Tomosvaryella*

Figs 61.19–26. Wings of Pipunculidae (dorsal views): (19) *Chalarus spurius* (Fallén) (non-Afrotropical); (20) *Cephalosphaera* (*Cephalosphaera*) *furcata* (Egger) (non-Afrotropical); (21) *Cephalops* (*Cephalops*) *vittipes* (Zetterstedt) (non-Afrotropical); (22) *Cephalops* (*Beckerias*) *pannonicus* (Aczél) (non-Afrotropical); (23) *Collinias fulvicaudus* De Meyer (non-Afrotropical); (24) *Microcephalops opacus* (Fallén) (non-Afrotropical); (25) *Eudorylas mutillatus* (Loew); (26) *Tomosvaryella sylvatica* (Meigen) (non-Afrotropical).

Abbreviations: aux vn – auxiliary vein; *bm* – basal medial cell; *br* – basal radial cell; *C* – costal vein; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *dm* – discal medial cell; *dm–m* – discal medial crossvein; M_1 – first branch of media; M_2 – second branch of media; M_4 – fourth branch of media; ptstg – pterostigma; R_1 – anterior branch of radius; r_{2+3} – third + fourth radial cells; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Sc* – subcostal vein.

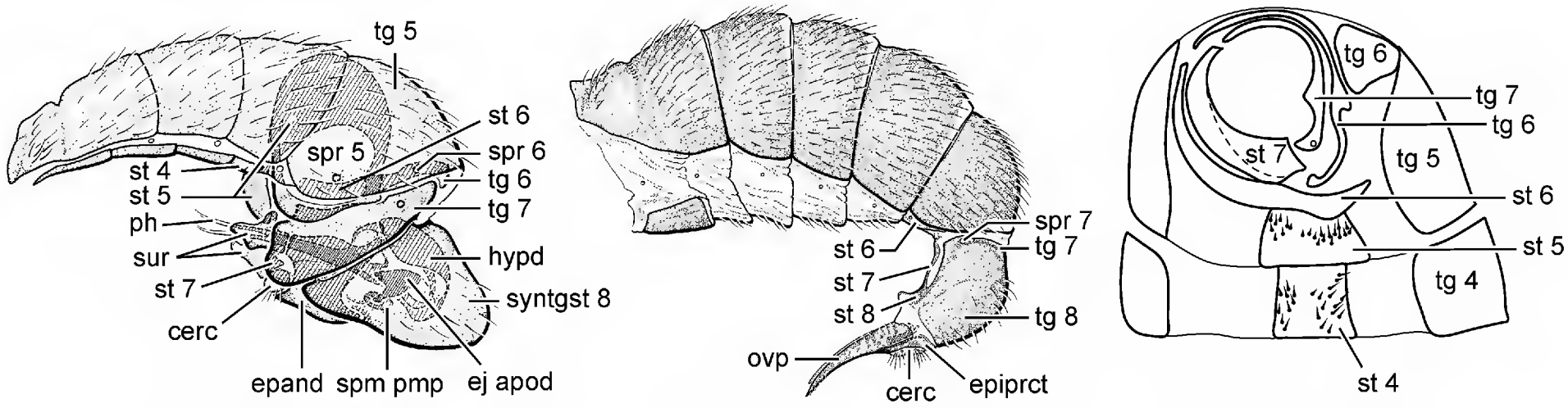
Empoasca fabae (Harris) (Cicadellidae), a major pest of alfalfa in the mid-western and eastern USA and Canada, involved exploration in Europe for natural enemies to be introduced into the USA (Jervis 1992) and included rearing of *Chalarus* Walker for release (Skevington & Marshall 1997).

Classification

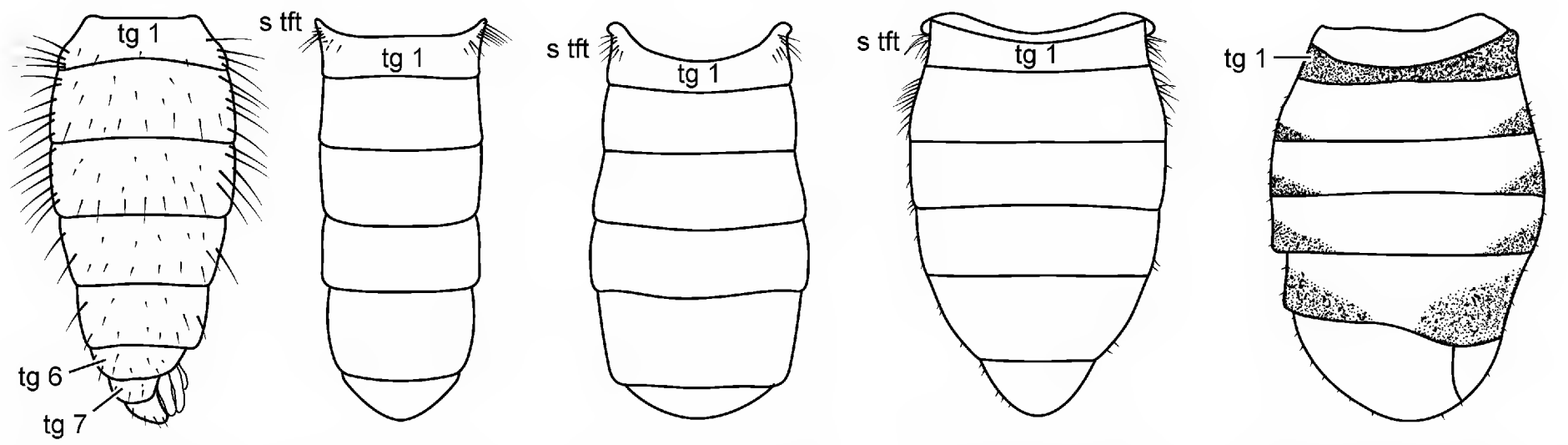
Pipunculidae are considered to be a monophyletic lineage and were traditionally treated as sister-group of the Syrphidae, in the superfamily Syrphoidea (Cumming *et al*. 1995; Griffiths 1972: 72; Woodley *et al*. 2009: 86). Recent evidence has challenged this hypothesis and suggested that Pipunculidae are the sister-group to the Schizophora (Pauli *et al*. 2018; Tachi 2014; Wiegmann *et al*. 2011).

Over 1,400 species of pipunculids are recognised globally and it is likely that over 2,700 species exist (De Meyer 1996*b*; De Meyer & Skevington 2000). Twenty-one extant genera are currently recognised in four subfamilies: Chalarinae, Nephrocerinae, Pipunculinae and Protonephrocerinae (De Meyer 1996*b*; De Meyer & Skevington 2000; Kehlmaier *et al*. 2014; Rafael & De Meyer 1992; Skevington & Yeates 2000). The subfamily Pipunculinae is divided into five tribes: Cephalopsini, Eudorylini, Microcephalopsini, Pipunculini and Tomosvaryellini (Rafael & De Meyer 1992).

Molecular analyses undertaken by Skevington & Yeates (2000) corroborated most of Rafael & De Meyer's (1992) phylogenetic results, except for the position of *Nephrocerus* and *Protonephrocerus*. These combined molecular data suggested that *Nephrocerus* is sister to the subfamily Chalarinae and *Protonephrocerus* is sister to the subfamily Pipunculinae. When these data were combined with the morphological dataset of Rafael & De Meyer (1992), *Nephrocerus* and *Protonephrocerus* were recovered between the early branching Chalarinae and terminal Pipunculinae, reflecting the hypothesis of Rafael & De Meyer,



27 *Dorylomorpha* ♂ 28 *Pipunculus* ♀ 29 Pipunculinae ♂



30 *Chalarus* ♂ 31 *Cephalops* (*Cephalops*) ♀ 32 *Cephalops* (*Semicephalops*) ♀ 33 *Claraeola* ♀ 34 *Clistoabdominalis* ♂

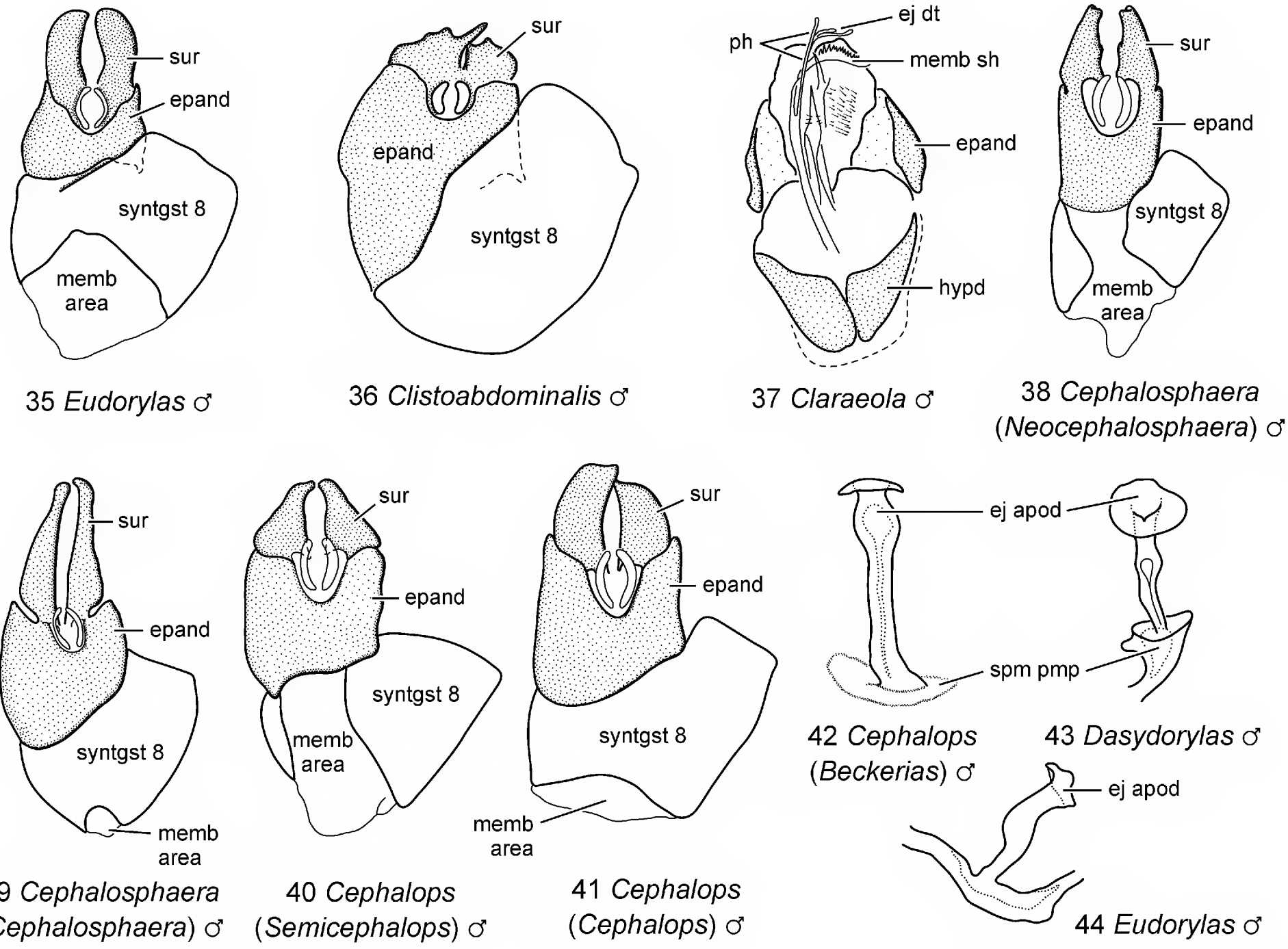
Figs 61.27–34. Abdomens of Pipunculidae: (27) male abdomen of *Dorylomorpha canadensis* Hardy, lateral view (non-Afrotropical); (28) female abdomen of *Pipunculus* sp., lateral view (non-Afrotropical); (29) diagrammatic representation of Pipunculinae male postabdomen, based upon *Dasydorylas eucalypti* (Perkins), ventral view (non-Afrotropical); (30) abdomen of *Chalarus* sp., dorsal view (non-Afrotropical); (31) same, *Cephalops* (*Cephalops*) sp., dorsal view (non-Afrotropical); (32) same, *Cephalops* (*Semicephalops*) sp. (non-Afrotropical); (33) same, *Claraeola* sp.; (34) same, *Clistoabdominalis helluo* (Perkins) (non-Afrotropical). Figs 27, 28 (after Hardy 1987, figs 8, 9), Figs 29, 33, 34 (after Skevington & Yeates 2000, figs 1D, 4I, 1E, respectively).

Abbreviations: cerc – cercus; ej apod – ejaculatory apodeme; epand – epandrium; epiprct – epiproct; hypd – hypandrium; ovp – ovipositor; ph – phallus; s tft – setal tuft; spm pmp – sperm-pump; spr – spiracle; st – sternite; sur – surstylus; syntgst – syntergosternite; tg – tergite.

with the difference that these two genera do not form a monophyletic group. More recent work on fossil pipunculids by Kehlmaier *et al*. (2014) supported this finding. Study of additional genes and morphological characters is required to further test these higher relationships. Generic concepts are relatively well-resolved, but more work is still required to clarify Eudorylini genera. Despite recent work on Eudorylini, problems remain within this large lineage (Kehlmaier 2005; Skevington & Yeates 2000).

Identification

Due to their small size, dark brown to black colouration and the paucity of external characters, pipunculid species are difficult to identify. It is particularly important to have male and female specimens from the same sample, in order to associate the sexes. For definitive identification it is necessary to dissect the male terminalia as described by Rafael & Skevington (2010: 795). In female specimens the ovipositor shape is often useful, but few other diagnostic characters are available, rendering an accurate identification to species-level difficult to impossible in some cases. Description of new species on the basis of females often further complicates the taxonomy of the family, especially if based on singletons and should be avoided unless new character systems are discovered for females. The writers encourage DNA barcoding (sequencing cytochrome oxidase I) of new species of pipunculids to facilitate association of sexes and larvae and to stabilise nomenclature across



Figs 61.35–44. Male terminalia of Pipunculidae: (35) syntergosternite 8, epandrium and surstyli of *Eudorylas acroapex* (Hardy), dorsal view; (36) same, *Clistoabdominalis namibiensis* Földvári; (37) male terminalia of *Claraeola nigripennis* (Hardy), ventral view; (38) syntergosternite 8, epandrium and surstyli of *Cephalosphaera* (*Neocephalosphaera*) *pallidifemoralis* (Hardy), dorsal view; (39) same, *Cephalosphaera* (*Cephalosphaera*) *magnispinosa* (Hardy); (40) same, *Cephalops* (*Semicephalops*) *saegeri* (Hardy); (41) same, *Cephalops* (*Cephalops*) *obtusus* (Hardy); (42) ejaculatory apodeme of *Cephalops* (*Beckerias*) *hemistilbus* (Hardy), dorsal view; (43) same, *Dasydorylas quasidorsalis* (Hardy); (44) same, *Eudorylas garambensis* (Hardy). Fig. 35 (after Földvári 2013, fig. 11B), Figs 36, 37, 43, 44 (after Földvári 2013, figs 6K, 4F, 9K, 22K, respectively).

Abbreviations: ej apod – ejaculatory apodeme; ej dt – ejaculatory duct; epand – epandrium; hypd – hypandrium; memb area – membranous area; memb sh – membranous sheath; ph – phallus; s – setae; spm pmp – sperm-pump; sur – surstylus; syntgst – syntergosternite.

wider geographical areas (see also Kehlmaier & Assmann 2010; Skevington *et al*. 2007).

Many pipunculids employ the landmark mating system, known as hilltopping (Skevington 2000: 29, 2001). Males vastly outnumber females at these mating sites, but occasionally pairs can be collected *in copula*. Other effective methods frequently employed to capture pipunculids include sweeping, Malaise trapping, and less successfully, the use of pan traps.

In order to secure the ground colour and tomentum of pipunculids, specimens should preferably be field-pinned for later double-mounting (see Chapter 2). Pinning fresh material killed with cyanide, chloroform or ethyl acetate is the easiest and a number of techniques can be used. Note that ethyl acetate and chloroform degrade DNA, so to allow for future sequencing it is best to use cyanide or simply freeze the specimens to kill them. The best method for obtaining views of the insect's terminalia involves double-mounting. Pinning through the right mesopleuron with a minuten pin, then pinning to Nu-poly strips is more expensive and time-consuming than point-mounting, but produces excellent specimens that are less likely to require dissection than other pinning techniques. Material collected into alcohol is preferably dried with a critical-point-drier and then point-mounted or glued directly to the side of a pin. Chemical drying using HMDS (hexamethyldisilazane) or ethyl acetate is also acceptable, although the former is hazardous to work with and causes shrinkage of specimens, while the latter potentially degrades DNA. For long-term storage, both dry and ethanol preservation is acceptable, although the writers recommend dry preservation, as ethanol preserved specimens (especially in 70% ethanol at room temperature) discolour over time, become brittle and are difficult to dissect when dried.

Terminology used to describe pipunculid morphology has varied considerably over time and between authors, but recent efforts have been made to standardise this language. Most of the current morphological terminology is illustrated here (Figs 27–29), but see Skevington & Yeates (2000) for a more thorough treatment of this topic.

The Afrotropical fauna was largely unknown until 1949, when D. Elmo Hardy published his monograph on Afrotropical Pipunculidae (Hardy 1949), followed by a series of papers over the next decade covering all material available at the time (see Skevington & De Meyer (2004) for a review of Hardy's taxonomic work on Pipunculidae and Afrotropical pipunculids in particular). Following Hardy's publication on Tanzanian Pipunculidae (Hardy 1960), no major study of the Afrotropical fauna for this group was conducted until 1990, when M. De Meyer began revising the fauna on a generic basis (De Meyer 1990*b*, 1992, 1993, 1996*a*), except the tribe Eudorylini, which was more recently revised by Földvári (2003*a*, *b*, 2013). The below identification key is largely based on Kehlmaier (2005), Rafael & Skevington (2010: 795) and Skevington & Yeates (2000). Two species are unplaced to any higher taxon (*"Pipunculus" flavicrus* Rapp, 1946 and *"Pipunculus" risbeci* Séguy, 1946). Type material needs to be consulted to resolve the identity of these taxa.

Key to genera of Afrotropical Pipunculidae

1. Head with ocellar setae distinct (Fig. 2); occiput narrow, scarcely projecting behind eyes (Fig. 2); head hemispherical (Fig. 2); margin of mesonotum and scutellum with strong setae (as in Fig. 8); wing venation incomplete, without crossvein *dm–m*, vein M_1 reduced (Fig. 19) (CHALARINAE) . . . . . *Chalarus* Walker

– Head with ocellar setae reduced or absent (e.g., Figs 3, 4); occiput swollen and plainly visible in lateral view (e.g., Figs 3, 4); head spherical (e.g., Figs 3, 4); margin of mesonotum and scutellum without strong setae (as in Fig. 9); wing venation complete, with crossvein *dm–m*, vein M_1 complete, reaching apical wing margin (e.g., Figs 20–26) (PIPUNCULINAE) 2

2. Head with face narrower than lower portion of frons (e.g., Fig. 6); frons inflated in lateral view (e.g., Fig. 4); antennal postpedicel small, slightly larger than pedicel (e.g., Fig. 4); wing with discal medial cell (*dm*) not expanded convexly on distal section after *r–m* crossvein (e.g., Figs 23, 24) (MICROCEPHALOPSINI) 3

– Head with face equal or subequal in width to lower portion of frons (e.g., Fig. 5); frons not inflated in lateral view (e.g., Fig. 3); antennal postpedicel distinctly larger than pedicel (e.g., Figs 3, 7); wing with discal medial cell (*dm*) expanded convexly on distal section after *r–m* crossvein (e.g., Figs 20–22; 25, 26) 4

3. Wing with auxiliary vein at base of third costal sector (Fig. 23) . . . . . *Collinias* Aczél

– Wing without auxiliary vein at base of third costal sector (Fig. 24) . . . . . *Microcephalops* De Meyer

4. Wing without pterostigma (Fig. 26) (TOMOSVARYELLINI) . . . . . *Tomosvaryella* Aczél

– Wing with pterostigma (e.g., Fig. 25) 5

5. Thorax with proepisternum with fan-like setal tuft (e.g., Fig. 10) (CEPHALOPSINI) 6

– Thorax with proepisternum bare (e.g., Fig. 11); only males identifiable to genus (EUDORYLINI). . . . 11

6. Wing with vein M_2 (Fig. 20) . . . . . *Cephalosphaera* Enderlein 7

– Wing without vein M_2 (Fig. 21). . . . . *Cephalops* Fallén 8

7. Hind tibia without tuft of longer setae apically (Fig. 12); male abdominal syntergosternite 8 with membranous area reaching epandrium (Fig. 38) . . . . . *Cephalosphaera* (*Neocephalosphaera* De Meyer)

– Hind tibia with tuft of longer setae apically (Fig. 13); male abdominal syntergosternite 8 with membranous area not reaching epandrium (Fig. 39) . . . . . .*Cephalosphaera sensu stricto*

8. Wing without vein *CuA+CuP* (Fig. 22); male terminalia with ejaculatory apodeme bottle-shaped (Fig. 42). . . . . .*Cephalops* (*Beckerias* Aczél)

– Wing with vein *CuA+CuP* (e.g., Fig. 21); male terminalia with ejaculatory apodeme not as above . . .9

9. Tibiae with strong median (on hind tibia, Fig. 17) and apical (on fore and mid tibiae, Fig. 16) spine-like setae; abdomen long and narrow (Fig. 31); male terminalia with syntergosternite 8 with membranous area not reaching epandrium (Fig. 41) . . . . . .*Cephalops sensu stricto*

– Tibiae without strong median (on hind tibia, Fig. 14) and apical (on fore and mid tibiae, Fig. 15) spine-like setae; abdomen broad and shortened (Fig. 32); male terminalia with syntergosternite 8 with membranous area reaching epandrium (Fig. 40) 10

10. Male with membranous area of syntergosternite 8 not reaching epandrium (as in Fig. 41); apical part of phallic guide strongly broadened . . . . . .*Cephalops* (*Parabeckerias* De Meyer)

– Male with membranous area of syntergosternite 8 reaching epandrium (Fig. 40); phallic guide not as above . . . . . .*Cephalops* (*Semicephalops* De Meyer)

11. Abdominal tergite 1 with dense setal tuft (Fig. 33); hind tibia usually with erect anteromedial setae over ½ length (Fig. 18); male terminalia with phallus partly clothed in small, but distinct setae or teeth, arranged on membranous sheath or on ejaculatory ducts (Fig. 37) . . . . . .*Claraeola* Aczél

– Abdominal tergite 1 bare (e.g., Fig. 34), or with row of setae (as in Fig. 30); hind tibia with 0–4 erect anteromedial setae only (as in Fig. 17); male terminalia with phallus without distinct setae or teeth. 12

12. Abdominal tergite 1 without lateral setal tuft or this minuscule (Fig. 34); male terminalia with ejaculatory apodeme very large and either 3-sided (balloon-shaped) or funnel-shaped; syntergosternite 8 enlarged (Fig. 36) . . . . . .*Clistoabdominalis* Skevington

– Abdominal tergite 1 with lateral setal tuft well-developed (as in Fig. 31); male terminalia with ejaculatory apodeme small; syntergosternite 8 of normal size (e.g., Fig. 35) 13

13. Hind tibia with erect anteromedial setae (as in Fig. 17); male terminalia with ejaculatory apodeme funnel-shaped (Fig. 43) . . . . . .*Dasydorylas* Skevington

– Hind tibia without outstanding anteromedial setae (as in Fig. 15); male terminalia with ejaculatory apodeme not funnel-shaped (Fig. 44) . . . . . .*Eudorylas* Aczél

Synopsis of the fauna

The following synopses are based on the works of De Meyer (1990*a*, *b*, 1992, 1993, 1996*a*, 2000), De Meyer & Földvári (2009: 238), De Meyer & Skevington (2000) and Földvári (2003*a*, *b*, 2013) and on unpublished material from various collections studied by the writers.

Although most genera have been revised in recent decades, the Afrotropical pipunculid fauna is still considered poorly known, as few regions have been sampled to any extent. New collecting events invariably turn up undescribed species (Basset *et al*. 2008; De Meyer 2000: 231; De Meyer & Földvári 2008).

To date, 10 genera and 169 species are recorded from the region. All genera that occur in the Afrotropics are known from other zoogeographical regions and have an extended distribution. The majority of species that occur in the Afrotropics are, however, endemic. The fauna of Madagascar has been the subject of one preliminary study (Hardy 1962) and seems to be characterised by a relatively high endemicity, with 12 endemic species, out of 22 recorded from the island (De Meyer 1993; Hardy 1962). By contrast, the fauna of the Arabian Peninsula appears to be entirely unexplored and no Pipunculidae are reported from those areas here considered as part of the Afrotropical Region (Yemen, Oman or United Arab Emirates), as was recently pointed out by Jahromi *et al*. (2017) in a checklist of the genus *Tomosvaryella* from the Middle East. Compared to the world fauna, the number of species is very limited. Due to poor sampling, it is expected that this is a clear underestimation and that many new species may occur in the region. As stated above, pipunculids are found in almost all terrestrial habitats, including canopy, lowland rainforest, dry forests, open areas, riparian regions and woodland edges; being more diverse in wet environments and along ecotones.

***Cephalops* Fallén** (Pipunculinae: Cephalopsini)**.** A genus of 180 described species occurring in all zoogeographical regions, except Antarctica. Thirty-three valid Afrotropical species are assigned to four subgenera (see De Meyer (1994) for subgeneric characters). Subgeneric diversity in the Afrotropics is as follows: *C.* (*Beckerias* Aczél) (two species), *Cephalops sensu stricto* (19 species, including the three *Wittella* species), *C.* (*Parabeckerias* De Meyer) (one species, *C. parvicornis* (Hardy, 1949)), *C.* (*Semicephalops* De Meyer) (10 species) and *Cephalops* subgenus *incertae sedis* (one species, *C. splendens* De Meyer, 1992). Representatives of the genus were revised by De Meyer (1990*a*, 1992). The former revised the genera *Beckerias* Aczél and *Wittella* Hardy. *Wittella* is currently placed in synonymy with *Cephalops sensu stricto* (Rafael & De Meyer

1992), while *Beckerias* is considered a subgenus of *Cephalops sensu lato* (De Meyer 1994). The biology and immature stages remain unknown. Afrotropical species can be identified using the identification key provided by De Meyer (1990*a*), for those species previously listed under *Beckerias* and *Wittella* and De Meyer (1992) for all other species.

***Cephalosphaera* Enderlein** (Pipunculinae: Cephalopsini)**.** A genus of 54 described species occurring in all zoogeographical regions, except Antarctica. Three described species occur in the Afrotropics (all known from Central Africa, with one doubtful occurrence from Zimbabwe). One species belongs to the subgenus *Cephalosphaera sensu stricto*, (*C.* (*C.*) *magnispinosa* (Hardy, 1950)), while the two other species, *C.* (*N.*) *collarti* (Hardy, 1952) and *C.* (*N.*) *pallidifemoralis* (Hardy, 1952), to the subgenus *Cephalosphaera* (*Neocephalosphaera* De Meyer). The biology and immature stages remain unknown. No identification key for Afrotropical species is currently available.

***Chalarus* Walker** (Chalarinae)**.** A genus of 43 described species occurring in all zoogeographical regions, except Antarctica (there are no described species in Australasia, but they are common there; e.g., Skevington 2000: 40). One species is recorded from the Afrotropics, *Ch. spurius* (Fallén, 1816), listed as widespread in the region by Hardy (1980; but see Jervis (1992) on the questionable identity of this record). Additional material is available from Namibia, but their identity is unknown. The biology and immature stages remain unknown. The genus has never been studied in detail for the Afrotropical Region, hence its distribution and species diversity remains unknown.

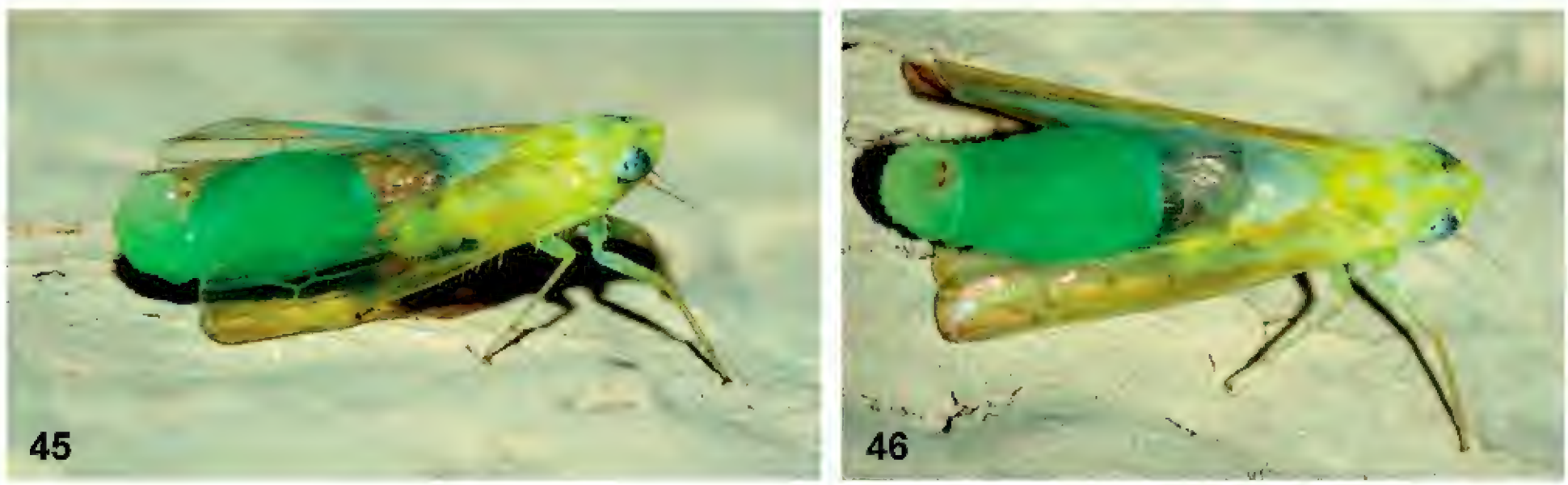
***Claraeola* Aczél** (Pipunculinae: Eudorylini)**.** A genus of 35 described species occurring in all zoogeographical regions, except the New World and Antarctica. Four species are recorded from the Afrotropics: *C. francoisi* (Hardy, 1952) from Burundi; *C. hadrosoma* (Hardy, 1962) from Madagascar; *C. nigripennis* (Hardy, 1949) from Cameroon, Democratic Republic of Congo and Uganda; and *C. stuckenbergi* Földvári, 2013, from Malawi and South Africa. The generic placement of one species, *C. francoisi*, remains uncertain (Földvári 2013; Skevington & Yeates 2000). The monotypic genus *Congomyia* Hardy was synonymised with *Claraeola* by Skevington & Yeates (2000). The biology and immature stages remain unknown. An identification key (to males only) of all Afrotropical species was provided by Földvári (2013).

***Clistoabdominalis* Skevington** (Pipunculinae: Eudorylini)**.** A genus of 47 described species occurring in all zoogeographical regions, except Antarctica. Four species are known from the Afrotropics, all from Southern Africa or islands in the western Indian Ocean, although one species, *C. nitidifrons* (which is only reported from Réunion Is. and Seychelles in the Afrotropics), is much more widespread in Asia and the near East (Földvári 2013). The biology and immature stages remain unknown. An identification key (males only) to all Afrotropical species was provided by Földvári (2013).

***Collinias* De Meyer** (Pipunculinae: Microcephalopsini)**.** A genus of nine described species occurring in the Afrotropical, Australasian/Oceanian and Oriental Regions. Only the single species, *C. fulvicaudus* De Meyer, 1996, recorded from Democratic Republic of Congo, Gabon and South Africa, occurs in the Afrotropics (Basset *et al.* 2008; De Meyer 1996*b*). The biology and immature stages of the species remain unknown. A detailed description and diagnostics were provided by De Meyer (1996*a*).

***Dasydorylas* Skevington** (Pipunculinae: Eudorylini)**.** A genus of 30 described species occurring in all zoogeographical regions, except Antarctica. Eight species are recorded from the Afrotropics, mainly in Southern and East Africa, with one species (*D. minymerus* (Hardy, 1962)) also recorded from Madagascar. The biology and immature stages of the species remain unknown. An identification key (males only) to all Afrotropical species was provided by Földvári (2013).

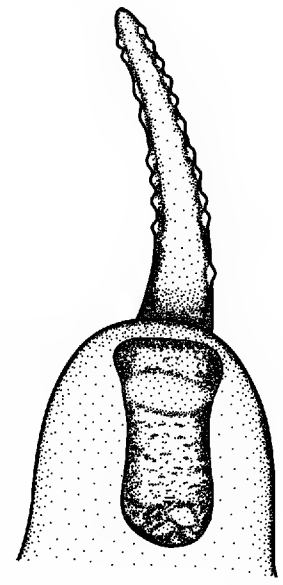
***Eudorylas* Aczél** (Pipunculinae: Eudorylini)**.** The largest genus in the family, with 417 described species occurring in all zoogeographical regions, except Antarctica. This is the best represented genus in the Afrotropics, with 62 described species and probably several undescribed ones. The majority of species are reported from East, Central and Southern Africa, with few records from West Africa and from the islands in the western Indian Ocean. The biology and immature stages of the species remain unknown. The Afrotropical species were revised by Földvári (2013), who provided an identification key to males of 53 species.



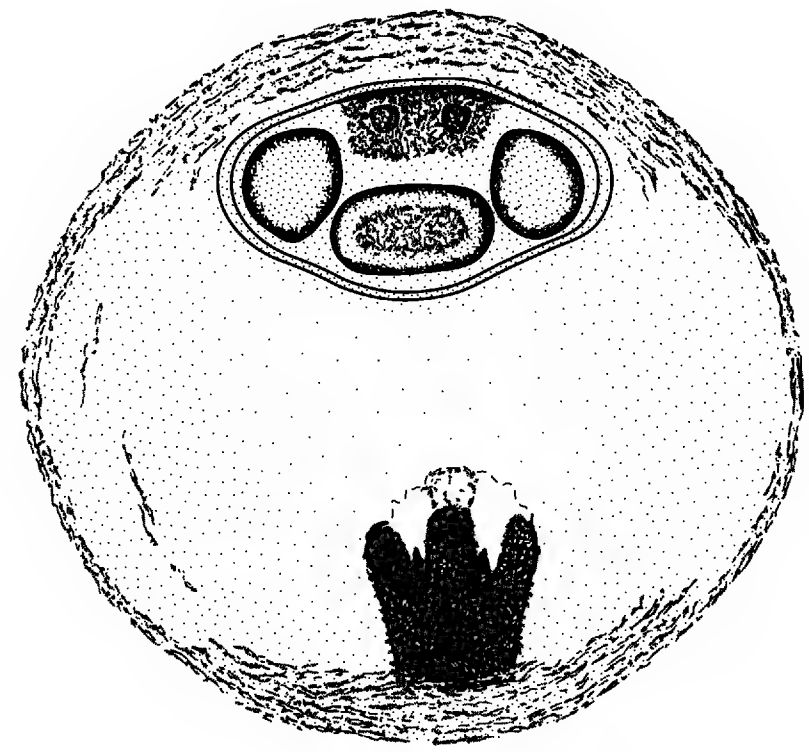
Figs 61.45–46. Immature stages of Pipunculidae: (45) living leafhopper (Hemiptera: Cidadellidae), parasitised by unidentified larva (presumed to be a pipunculid), lateral view (non-Afrotropical); (46) same, dorsolateral view. Figs 45, 46 (photographs © K. Hall).

***Microcephalops* De Meyer** (Pipunculinae: Microcephalopsini)**.** A genus of 32 described species occurring in all zoogeographical regions, except Antarctica. Nine species occur in the Afrotropics. The majority of the species is reported from Central, East and Southern Africa. The biology and immature stages of the species remain unknown. All nine species were discussed and an identification key provided by De Meyer (1996a).

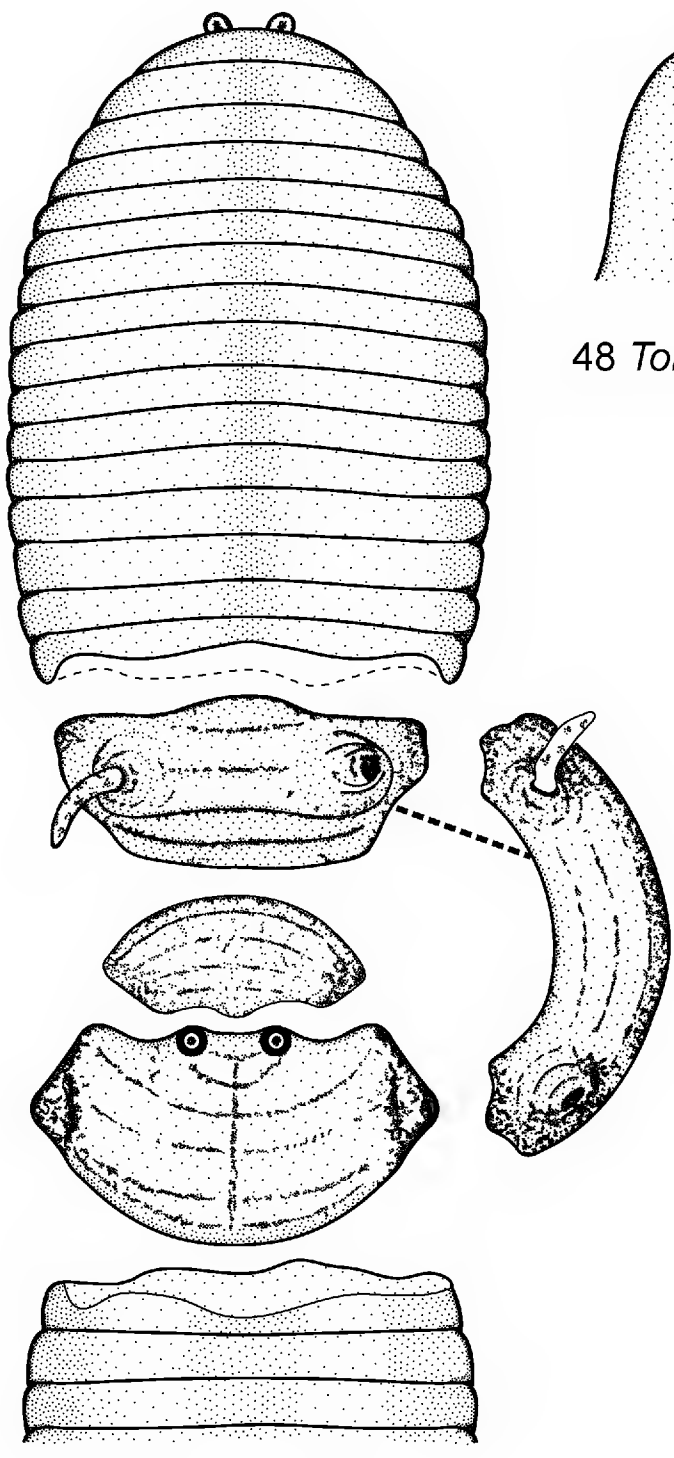
***Tomosvaryella* Aczél** (Pipunculinae: Tomosvaryellini)**.** A genus of 280 described species occurring in all zoogeographical regions, except Antarctica. This is the second largest genus in the region, with 43 recorded species and probably a number of undescribed species (Bassett *et al*. 2008; De Meyer & Földvári 2008). Species are recorded from all areas in the Afrotropical region. The biology and immature stages of the species remain unknown, except for the puparium of *T. singula* Hardy, 1950 which was described by Kirk-Spriggs (1988). The Afrotropical species were revised and an identification key provided by De Meyer (1993), with an addition in De Meyer & Földvári (2008) to include *T. olmii* De Meyer & Földvári, 2008.



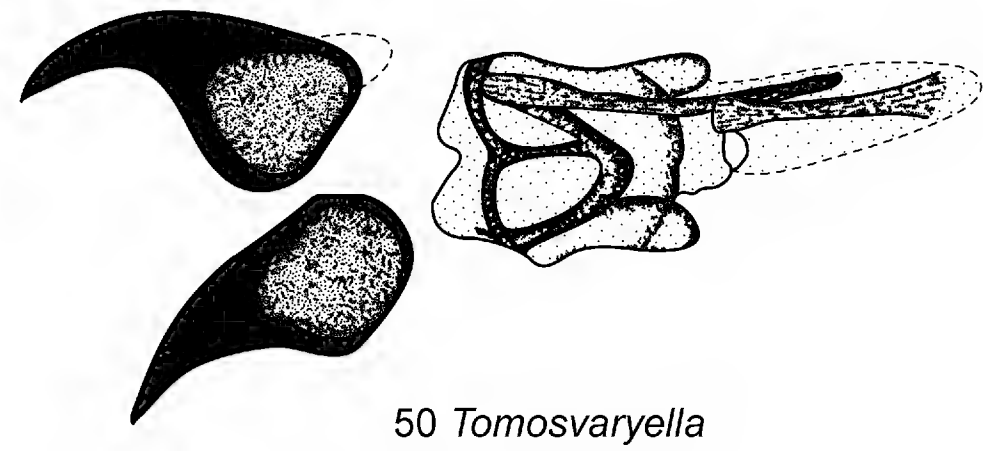
48 *Tomosvaryella*



49 *Tomosvaryella*



47 *Tomosvaryella*



50 *Tomosvaryella*

Figs 61.47–50. Immature stages of Pipunculidae: (47) habitus of puparium of *Tomosvaryella singula* Hardy, dorsal view (indicating detached puparial plates in order of attachment and below ventral view of puparium); (48) same, detached pupal prothoracic spiracle, lateral view; (49) same, puparium caudal view; (50) same, cephaloskeleton, lateral view. Figs 47–50 (after Kirk-Spriggs 1988, figs 5, 7, 3, 8, respectively).

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MICROPEZIDAE 62

(Stilt-legged Flies)

Stephen A. Marshall

Fig. 62.1. Female of *Aristobatina rufithorax* (Enderlein) (Tanzania) (photograph © S.A. Marshall).

Diagnosis

Medium- to large-sized (body length: 4–20 mm) acalyptrate flies, with distinctively long mid and hind legs (Figs 1, 6).

Head (Figs 2–4, 7–9) with antennal arista bare to plumose, inserted dorsobasally; ocelli often displaced anteriorly (Figs 3, 8); ocellar setae and vibrissae absent (Fig. 7); inner and outer vertical and postocellar setae present or absent (inner vertical rarely absent); 1 upper fronto-orbital (Fig. 4), 1–2 lower fronto-orbital setae sometimes present; frontal vitta usually distinct, often elevated.

Thorax (Figs 2–5, 8) usually elongate, often tapered anteriorly; chaetotaxy variable, but anepisternal setae absent, katepisternum usually with row or cluster of setae posteriorly; most Afrotropical species (all but 1 introduced micropezine and 1 Mascarene eurybatine), with distinctive vertical, fan-like row of katepisternal setae (Figs 3, 4). Scutellum (Fig. 8) usually with 1 pair of apical setae. Wing (Figs 10–12) with subcostal

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2021. Manual of Afrotropical Diptera. Volume 3. Brachycera—Cyclorrhapha, excluding Calyptratae. *Suricata* 8. South African National Biodiversity Institute, Pretoria; pp. 1507–1515.

2 *Micropeza*

3 *Hybobata*

4 *Cothornobata*

Figs 62.2–4. Habitus of Micropezidae (lateral views): (2) *Micropeza* sp.; (3) *Hybobata triannulata* Macquart; (4) *Cothornobata paieroi* Li.

Abbreviations: frorb s – fronto-orbital seta; kepst – katepisternum; kepst s – katepisternal seta; oc – ocellus.

vein (*Sc*) complete (Fig. 11); costal vein (C) unbroken; cell *cua* complete; veins R_{4+5} and M_1 convergent towards wing tip. Legs with fore coxa usually widely separated from mid coxa; tibiae sometimes with dorsal setae, but never with distinct preapical seta.

Abdomen (Figs 13, 14) of most males with prominent forked posteromedial process on sternite 5 (Fig. 14, inset); male terminalia of Micropezinae (South Africa) and Eurybatinae (Mascarene Is.) with surstyli, Taeniapterinae (Figs 13, 15) without; distiphallus generally divided into stout basal part, short swelling (phallic bulb) and generally slender distal part (highly variable, sometimes absent); female abdominal tergite and sternite 7 fused to form rigid tubular oviscape housing ovipositor; ventral receptacle usually present, but varying from very small to very large; most species with 2 + 1 spermathecae (Fig. 16), but some species with 2 + 2; structure of spermathecae and associated ducts highly variable.

Neriidae (see Chapter 63), the long-legged flies most similar to Micropezidae, have an apical antennal arista in contrast to the dorsobasal arista of Micropezidae and have ocelli placed at the back of the head, more or less level with the posterior margin of the eye. Neriids also lack the forked posteromedial process found on the male sternite 5 of most micropezids, usually have vibrissae or short stout setae at the vibrissal angle and often have spine-like setae on the fore femur.

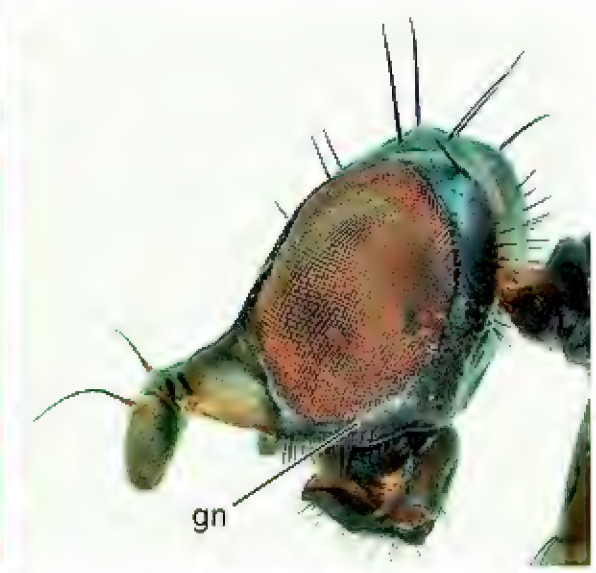
Biology and immature stages

Micropezids are common flies in humid tropical and temperate habitats, where they are often exposed on leaves or similar surfaces. Many species closely resemble sympatric Hymenoptera, such as ants (Formicidae), spider wasps (Pompilidae) and ichneumonoid wasps. The fore legs, which are much shorter than the mid legs and hind legs, are usually similar in pigmentation to the antennae of sympatric ichneumonid or pompilid wasps and are typically waved in front of the body in an antenna-like fashion. Micropezids often engage in elaborate courtship behaviours, involving conspicuous male displays, transfer of regurgitated fluids from the male to the female and other complex behaviours (Wheeler 1924), but the biology of Afrotropical species is poorly known.

Micropezids have been reared from a variety of decomposing plant material, occasionally including dung and rotting fruit, but more often decaying logs or roots. Several species, including species in the endemic Afrotropical genus *Aristobatina* Verbeke, have been observed ovipositing in beetle-borings in fallen trees (Marshall 2014) and *Cephalosphen conifrons* (Bigot, 1886) has been reared from rotting wood (Hennig 1936). The eurybatine *Paraeurybata taeniata* (Macquart, 1843) oviposits in large rotting logs in old growth forests of the Mascarene Is. (Marshall 2019). Some species of *Mimegralla* Rondani develop in tuberous roots (Steyskal 1964) and known *Micropeza*

5 *Glyphodera*

6 *Paramimegralla*



7 *Cephalosphen*

8 *Erythromyiella*

9 *Tanypomyia*

Figs 62.5–9. Habitus, heads and heads and thoraces of Micropezidae: (5) *Glyphodera* sp.; (6) *Paramimegralla steineri* (Barraclough); (7) *Cephalosphen* sp.; (8) *Erythromyiella rufa* (Hennig); (9) *Tanypomyia venusta* (Enderlein).

Abbreviations: gn – gena; msm – mesonotum; oc – ocellus; pal s – postalar seta; sctl – scutellum.

Meigen larvae develop in fresh, healthy root nodules of several leguminous plants (Müller 1957). Adults of many micropezid species are attracted to dung, some are attracted to artificial honeydew (honey and water sprayed on leaves) and a few species are attracted to decomposing fruit. Some Micropezidae, especially a few species of *Hybobata* Enderlein and *Mimegralla*, are associated with highly disturbed areas. Other taxa are usually associated with native forests.

Most of the relatively few known micropezid larvae (Figs 17, 18) have two protuberant and dorsally pointed posterior spiracular plate processes, each bearing a spiracular disc with three or four spiracular opening (the disc has numerous pores in one Nearctic species and the spiracles are vestigial in one Australasian species). The prothoracic spiracles (Fig. 17) are usually fan-shaped, but are sometimes reduced or divided into two lobes. The cephaloskeleton (Figs 20, 21) has the mouthhooks bluntly rounded apically, the intermediate sclerite, parastomal bar and basal sclerite well-developed and the floor of the pharynx forming a cibarial filter. Larvae are unknown for Afrotropical genera, but much of what is known about micropezid larvae elsewhere is summarised by Ferrar (1987). The puparium is illustrated in Fig. 19.

Economic significance

The native Afrotropical species of Micropezidae apparently have no significant agricultural or medical importance, but some widespread species of *Mimegralla* develop in rhizomes and are pests of ginger and turmeric. The only *Mimegralla* in the Afrotropical Region is an introduced species in Mauritius, *Mimegralla splendens* (Wiedemann, 1830), where it probably develops in roots of Taro, *Colocasia esculenta* (L.) Schott (Araceae). The only *Micropeza* species in the Afrotropical Region is an introduced species, *Micropeza corrigiolata* (L., 1767), that develops in root nodules of legumes.

Classification

Micropezidae belong to the superfamily Nerioidea, along with the non-Afrotropical families Cypselosomatidae and Pseudopomyzidae and the widespread family Neriidae. The family Micropezidae is currently divided into six subfamilies, of which three occur in the Afrotropical Region, but only one, the very large subfamily Taeniapterinae, occurs naturally in the continental Afrotropics. The primarily Pacific-Oriental subfamily Eurybatinae is only known in the Afrotropical Region from one monotypic genus (*Paraeurybata* Marshall), endemic to Mauritius and Réunion Is. (Marshall 2019). The mostly New World and Holarctic subfamily Micropezinae is only known in the Afrotropics from South African records of an introduced European species of *Micropeza* (Barraclough 1996).

The generic classification of the world Micropezidae, especially the subfamily Taeniapterinae, remains unstable and several of the larger genera, such as *Mimegralla*, are still defined only on the basis of superficial similarity (Marshall 2010). The large, ill-defined genus *Mimegralla* was until recently considered to include Afrotropical species, even though there is an existing name (*Hybobata* Enderlein) for the African clade treated as part of *Mimegralla* by Steyskal (1980: 580). *Hybobata*, resurrected from synonymy with *Mimegralla* by Marshall (2017), is the largest micropezid genus in the Afrotropics, followed closely by the Afrotropical genera *Glyphodera* Enderlein and *Paramimegralla* Hennig (18 species each). The smaller endemic Afrotropical taxa *Cephalosphen* Hennig (7 species), *Courtoisia* Barraclough (2) and *Erythromyiella* Verbeke (2) share a number of apparent synapomorphies, such as the unusual doubling of the postalar seta and the "peristomal fringe" of closely spaced setae on the anterior part of the gena and probably form a single clade. The fauna of Madagascar was until recently thought to include two endemic genera as well as species in the widespread genera *Mimegralla* and *Rainieria* Rondani, but Marshall (2017) concluded that the Malagasy micropezid fauna includes only two genera: the endemic *Paramimegralla* (16 species) and two species of the Afrotropical genus *Hybobata*. The Afrotropical micropezid fauna as a whole is thus almost entirely endemic to the region at the generic level.

Identification

Despite their relatively large size and conspicuous behaviour, most micropezids are not easily identified, many species remain undescribed and many genera require revision. Verbeke's (1951) treatment of the Micropezidae of Democratic Republic of Congo is the single most important work on Afrotropical Micropezidae and includes identification keys to genera and species, as well as descriptions of 17 new species. Barraclough (1991, 1992*a*, *b*, 1993, 1996) provided treatments of the Malagasy, Mascarene and Southern African faunas, adding four new species and one new regional record to the 61 Afrotropical micropezid species listed by Steyskal (1980). Marshall (2014, 2017) provided identification keys to species of *Aristobatina* and micropezid species of Madagascar, respectively, the latter including an identification key to all species of *Paramimegralla*. Micropezidae are best direct- or micro-pinned in the field for later double-mounting (see Chapter 2).

Key to genera of Afrotropical Micropezidae

1. Head without fronto-orbital setae (Fig. 2); wing vein *CuA* straight; wing cells *bm* and *dm* confluent (crossvein *bm–m* absent) (Fig. 10); upper calypter bare or with small, inconspicuous setulae only (MICROPEZINAE) (South Africa) . . . . . .*Micropeza* Meigen

– Head with fronto-orbital setae (1–3; often small, e.g., Fig. 4); wing vein *CuA* sloped distally; cells *bm* and *dm* separate (crossvein *bm–m* present) (Fig. 11); upper calypter (= axillary cord), with tightly packed comb of short setae (continental Afrotropics and Indian Ocean islands) 2

2. Thorax with katepisternum with only 3 or 4 large posterior setae (as in Fig. 4), not forming fan-like row; subscutellum strongly developed; male terminalia with surstylus (EURYBATINAE) (Mascarene Is.). . . . . *Paraeurybata* Marshall

– Thorax with katepisternum with dense, fan-like, vertical row of posterior setae (e.g., Fig. 3); subscutellum undeveloped; male terminalia without surstylus (TAENIAPTERINAE) (continental Afrotropics and Indian Ocean islands) 3

3. Thorax with anterior part of mesonotum forming long "neck", anterior margin with 2 variously developed lobes or prominent processes (Fig. 5); head with only inner vertical setae (without postocellar and outer vertical setae); postalar seta reduced or absent (continental Afrotropics) . . . . *Glyphodera* Enderlein

– Thorax with anterior part of mesonotum not forming long "neck", anterior margin of mesonotum simple, not projecting into 2 prominent processes (e.g., Fig. 8); head with postocellar and/or outer vertical seta present (*i*.e., upper part of posterior portion of head with 2 or 3 pairs of setae); 1 or 2 well-developed postalar setae present (continental Afrotropics and Indian Ocean islands) 4

4. Thorax with 2 postalar setae (e.g., Fig. 8); head with face strongly projected anteriorly; anteroventral margin of gena with closely spaced row of short setae (e.g., Fig. 7) 5

– Thorax with 1 postalar seta; head with face not strongly projected anteriorly; anteroventral margin of gena with only sparse setulae, not forming dense marginal row 7

5. Head without inner and outer vertical setae; thorax with anterior margin of mesonotum forming prominent conical extension; wing membrane mostly dark, with isolated pale "windows" (Mascarene Is. [possibly extinct]) . . . . . *Courtoisia* Barraclough

– Head with inner and outer vertical setae; thorax with anterior of mesonotum rounded, not conspicuously produced; wing membrane mostly clear, usually with dark fasciae (Fig. 12) (continental Afrotropics) 6

6. Ground colour black; head with frontal vitta not differentiated from rest of frons (continental Afrotropics) . . . . . *Cephalosphen* Hennig

– Ground colour yellow; head with frontal vitta clearly differentiated from rest of frons (Fig. 8) (continental Afrotropics) . . . . . *Erythromyiella* Verbeke

7. Head without postocellar setae; ocelli positioned near top of head, much closer to vertex than to lower frons 8

– Head with postocellar setae; ocelli position variable, sometimes distant from vertex, often midway between anterior margin of frons and back of head 9

8. Head with lunule and basal ½ of palpus not contrasting in colour with face; thorax with mesonotum $< 2 \times$ as long as wide; robust flies; male terminalia with phallus short and broad, with curved basal distiphallus and very short, stout distal distiphallus beyond small phallic bulb (continental Afrotropics and Indian Ocean islands) . . . . . *Hybobata* Enderlein

– Head with lunule and basal ½ of palpus orange, contrasting in colour with shiny black face; thorax with mesonotum $> 2 \times$ as long as wide; gracile flies; male terminalia with phallus elongate, basal distiphallus straight, distal distiphallus long and thin (Mauritius [introduced]) . . . . . *Mimegralla* Rondani

9. Head with outer vertical seta; frontal vitta very broad and convex, tapered to point behind ocelli (Fig. 9); ocelli positioned near vertex (continental Afrotropics) . . . . . *Tanypomyia* Verbeke

– Head with or without outer vertical seta; frontal vitta not swollen and broad, either weakly differentiated or swollen part small; ocelli positioned far anterior to vertex. 10

10. Head with frontal vitta with swollen part restricted to upper ½, lower frons flat; outer vertical setae present or absent, if present, then frontal vitta with relatively small, dark swollen area restricted to upper part of frons, lower part extensively orange; male terminalia with basiphallus elongate, extending posteriorly beyond base of distiphallus (continental Afrotropics) . . . . . *Aristobatina* Verbeke

– Head with frontal vitta flat or concave, weakly differentiated, never with swollen oval restricted to upper ½; with outer vertical seta; male terminalia with basiphallus not extending posterior to base of distiphallus (Madagascar) . . . . . *Paramimegralla* Hennig

Synopsis of the fauna

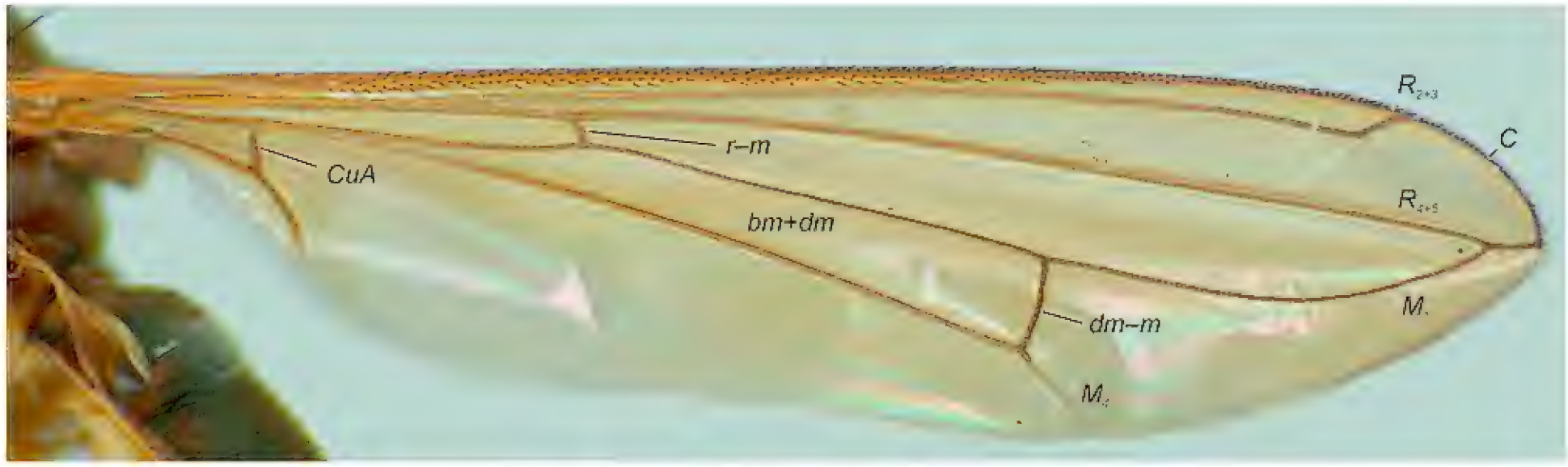
The 81 species currently recorded from the Afrotropical Region probably represent only a fraction of the fauna. Three out of the four micropezid species collected during one short field trip to Tanzania, for example, were new (Marshall 2014). The small South African fauna is probably entirely known and J. Verbeke monographed large collections from Central and West Africa in the 1950s, but the Micropezidae elsewhere in the continent remain poorly known. The Malagasy fauna was reviewed by Marshall (2017).

***Aristobatina* Verbeke** (Taeniapterinae)**.** An endemic genus of six described species, occurring in East and Southern Africa. The genus was diagnosed by Verbeke (1951) and Barraclough (1996), on the basis of two described species, both

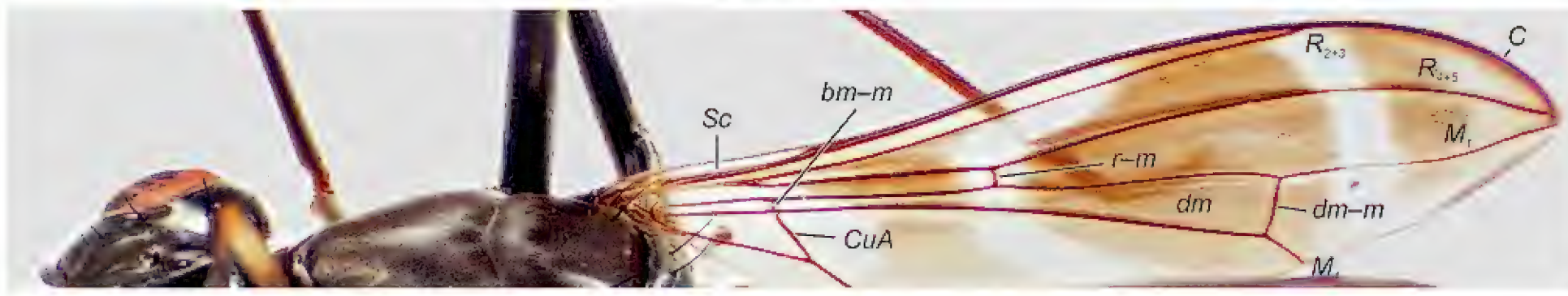
characterised by a partially brick red ground colour and the absence of outer vertical setae. Three subsequently described species from the Undzungwa Mountains (Eastern Arc Mountains) of Tanzania have inner and outer vertical setae and are mostly black with at most only the posterior half of the scutum dark brick red (Marshall 2014). Immature stages remain unknown, although Marshall (2014) documented oviposition in fallen trees. The most recent identification key to Afrotropical species was provided by Marshall (2014).

***Cephalosphen* Hennig** (Taeniapterinae)**.** An endemic genus of seven described species widespread in the continental Afrotropics. It is probably closely related to the small genera *Courtoisia* and *Erythromyiella*, both of which also have duplicated postalar setae. Barraclough (1996) recorded the habitat of the South African species, *C. conifrons,* as "sylvicolous" and described it as resting on sunlit areas of bark and Hennig (1936) recorded the same species as reared from rotting wood. An identification key to species was provided by Verbeke (1951).

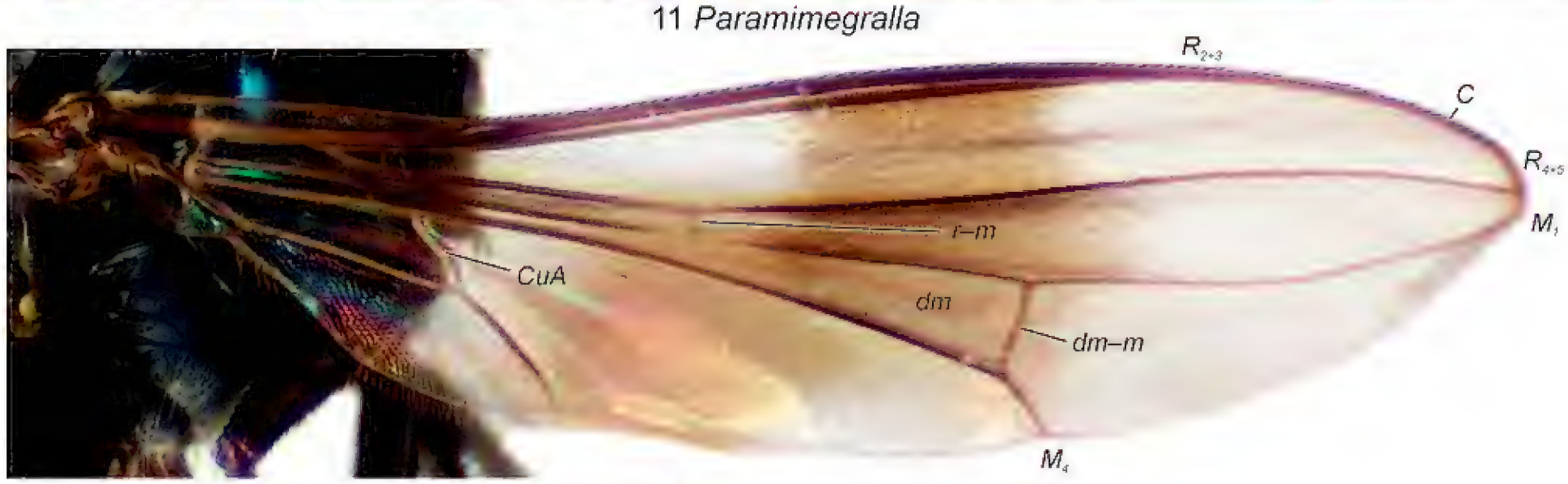
***Courtoisia* Barraclough** (Taeniapterinae)**.** An endemic genus of two described species, *C. apicalis* (Macquart, 1851) and *C. trinotata* (Macquart, 1851), confined to the Indian Ocean islands of Mauritius and Réunion Is. Biology and immature



10 *Micropeza*



11 *Paramimegralla*



12 *Cephalosphen*

Figs 62.10–12. Wings of Micropezidae (dorsal views): (10) *Micropeza bilineata* Wulp (non-Afrotropical); (11) *Paramimegralla campanula* Marshall; (12) *Cephalosphen* sp.

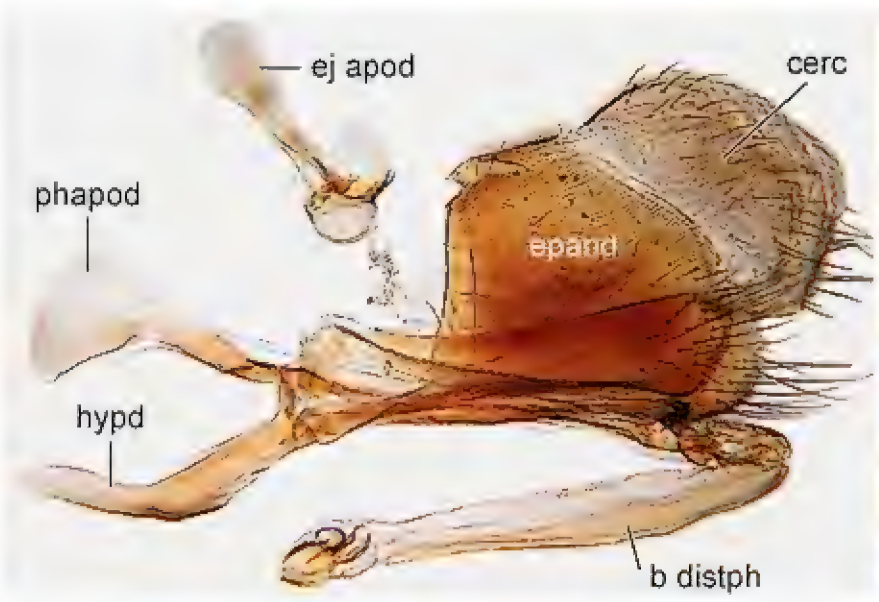
Abbreviations: *bm+dm* – basal medial cell + discal medial cell; *bm–m* – basal medial crossvein; *C* – costal vein; *CuA* – anterior branch of cubital vein; *dm* – discal medial cell; *dm–m* – discal medial crossvein; M_1 – first branch of media; M_4 – fourth branch of media; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Sc* – subcostal vein.

stages remain unknown. Barraclough (1993) provided an identification key to distinguish the two species. This genus has only been collected once since the 19th century and may well be extinct.

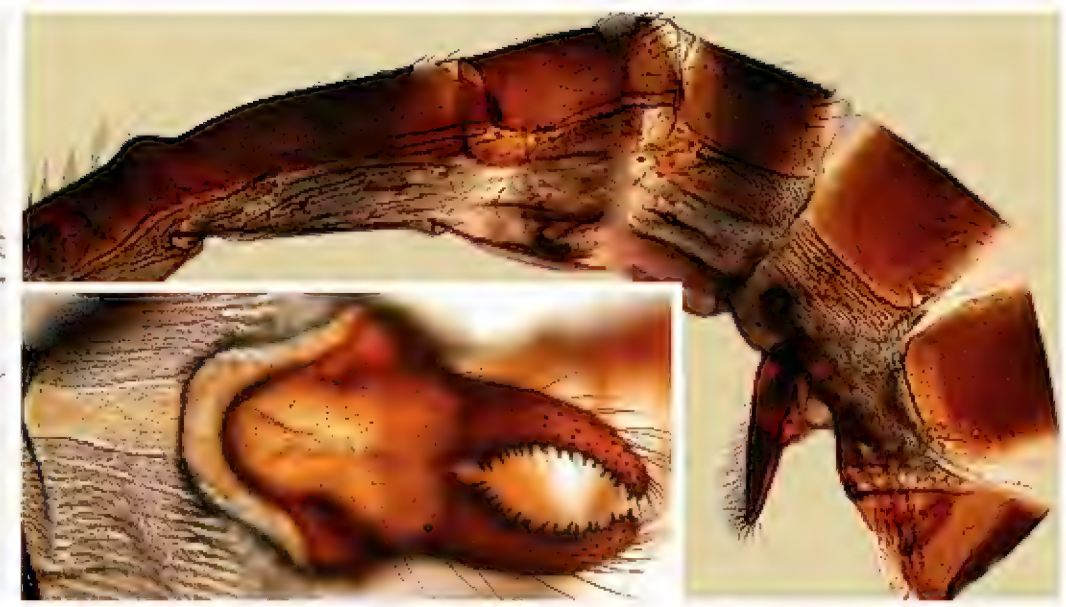
***Erythromyiella* Verbeke** (Taeniapterinae)**.** An endemic genus of two species, probably closely related to *Cephalosphen* and *Courtoisia*. One species, *E. rufa* (Hennig, 1935), is widespread from South Africa north to Liberia and the other, *E. tuberculata* (Hennig, 1935), was described from Ghana. Both are unusually pale and yellowish and *E. tuberculata* differs from *E. rufa* in lacking postocellar setae. The name *Erythromyiella* was first used by Hennig (1935), without specific type designation. Verbeke (1951) validated the genus by designating *Aristobatina rufa* Hennig, 1935 as the type species. Biology and immature stages remain unknown. Characters distinguishing the two species were provided by Verbeke (1951).

***Glyphodera* Enderlein** (Taeniapterinae)**.** An endemic genus of 18 described species occurring in tropical forests of Central, East and West Africa. *Glyphodera* is a distinctive genus with a prominently bilobed anterior thoracic margin. Biology and immature stages remain unknown. Identification keys to species-groups and species were provided by Verbeke (1951).

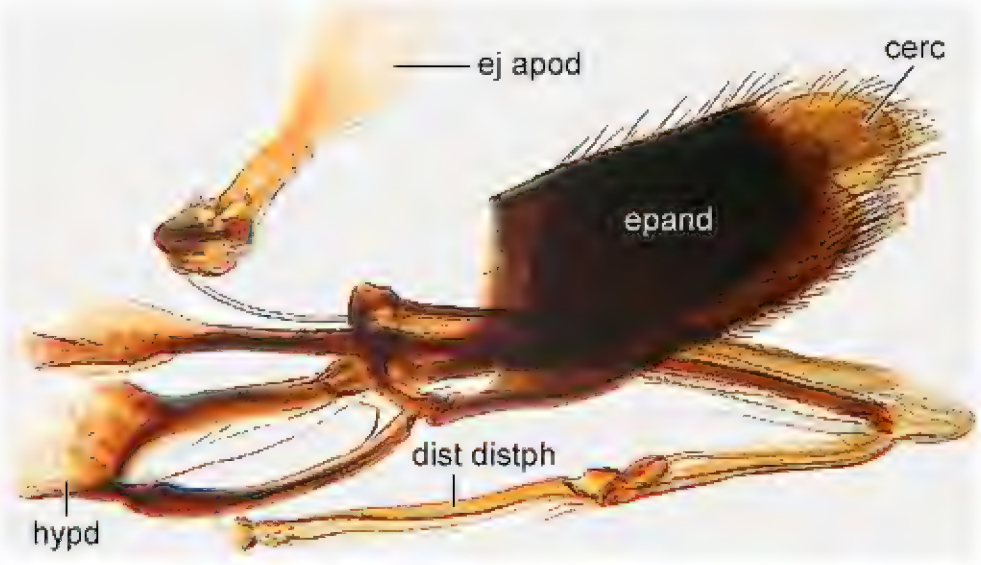
***Hybobata* Enderlein** (Taeniapterinae)**.** An endemic genus of 23 species, widely distributed in the continental Afrotropics, Bioko Is. (Equatorial Guinea) and Madagascar. Most of the Afrotropical species treated as *Mimegralla* by Steyskal (1980: 580) belong to *Hybobata*. Verbeke (1951) divided the Afrotropical species that Steyskal later treated as *Mimegralla* into the genera *Cyclosphen* Frey and *Tanypomyia* Verbeke. He also divided the entire Taeniapterinae into two clades, with *Tanypomyia* in one of these clades and *Cyclosphen* in the other. Steyskal's (1980: 580) treatment of both of these genera as synonyms of *Mimegralla* was unjustified, as *Tanypomyia* is more closely related to *Aristobatina*. Steyskal was, however, probably correct in treating *Cyclosphen* as a junior subjective synonym of *Mimegralla*, as both genera have similar South-east Asian type species, each belonging to a clade not represented



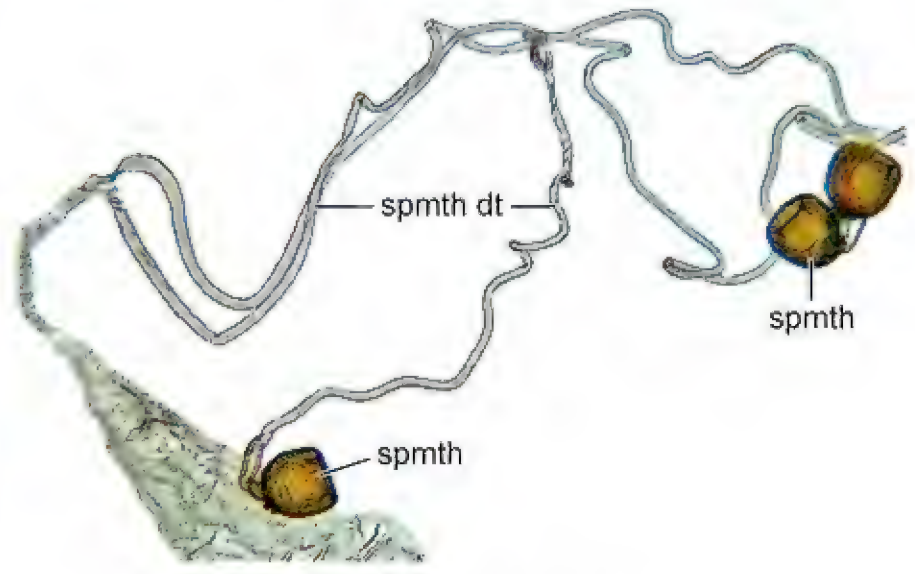
13 *Paramimegralla* ♂



14 *Paramimegralla* ♂



15 *Paramimegralla* ♂



16 *Paraeurybata* ♀

Figs 62.13–16. Male and female terminalia of Micropezidae: (13) male terminalia of *Paramimegralla stiltodes* Marshall, left lateral view; (14) same, entire abdomen lateral view (inset: detail of sternite 5, ventral view); (15) male terminalia of *P. zinzala* Marshall, left lateral view; (16) female spermathecae and associated ducts of *Paraeurybata taeniata* (Macquart), lateral view.

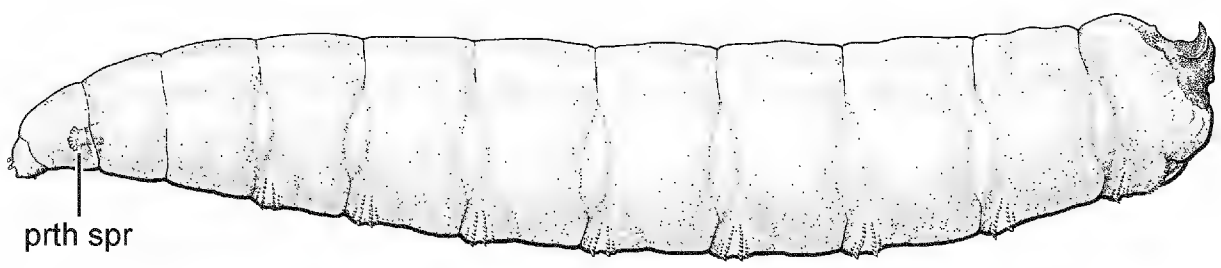
Abbreviations: b distph – basal distiphallus; cerc – cercus; dist distph – distal distiphallus; ej apod – ejaculatory apodeme; epand – epandrium; hypd – hypandrium; phapod – phallapodeme; spmth – spermatheca; spmth dt – spermathecal ducts.

in the Afrotropics. The Afrotropical clade treated by Verbeke (1951) as *Cyclosphen* includes the type of *Hybobata*. *Hybobata* is, therefore, the correct name for the Afrotropical *Cyclosphen sensu* Verbeke (1951) and thus for the Afrotropical *Mimegralla sensu* Steyskal (1980: 580). Steyskal (1980) listed 26 Afrotropical species in the genus *Mimegralla*, of which 24 belong in *Hybobata* (two belong in *Tanypomyia*). Barraclough (1996) suggested that some of the Afrotropical species described by Verbeke (1951, 1955) are probably synonyms, but provided no evidence in support of that claim. All of the *Hybobata* species for which male terminalia have been examined have a strikingly short and broad phallus, in contrast to the elongate distiphallus of *Mimegralla*. Biology and immature stages remain unknown. An identification key to species and species-groups of the genus (as *Cyclosphen*) was provided by Verbeke (1951).

***Micropeza* Meigen** (Micropezinae)**.** A large, widespread genus of 84 described species occurring in the Nearctic, Neotropical and Palaearctic Regions. A single species, *M. corrigiolata*, occurs in the Afrotropics and likely represents an introduction into South Africa from Europe. *Micropeza* species with known larvae develop in the root nodules of legumes. *Micropeza corrigiolata* was included in an identification key to South African species of Micropezidae by Barraclough (1996).

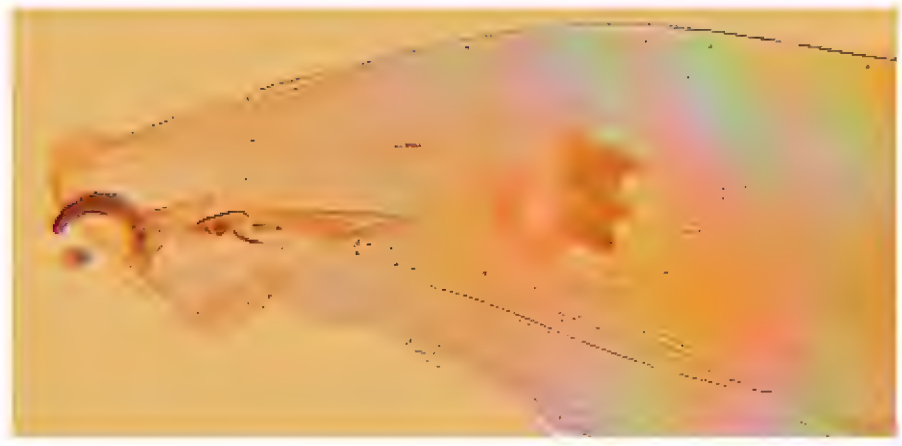
***Mimegralla* Rondani** (Taeniapterinae)**.** A large, poorly known genus of *ca* 60 species occurring in the Australasian, Oriental and Palaearctic Regions. All previous records of the genus from the Afrotropical Region are in error, as they refer to species that belong in *Hybobata* and *Tanypomyia*, but one species, *M. splendens*, was recently recorded from coastal Mauritius in the Indian Ocean (Marshall 2019). This species was probably introduced from India and possibly develops in the roots of Taro. This represents the first and only record of *Mimegralla* from the Afrotropical Region. *Mimegralla splendens* was included in an identification key to the Micropezidae of Mauritius by Marshall (2019).

***Paraeurybata* Marshall** (Eurybatinae)**.** An endemic monotypic genus, with the single described species, *P. taeniata*, confined to the Indian Ocean islands of Mauritius and Réunion Is. McAlpine (1975) suggested that this Mascarene species belongs in the otherwise Australasian/Oriental genus *Cothornobata* Czerny and Barraclough (1992*b*) formally transferred it to

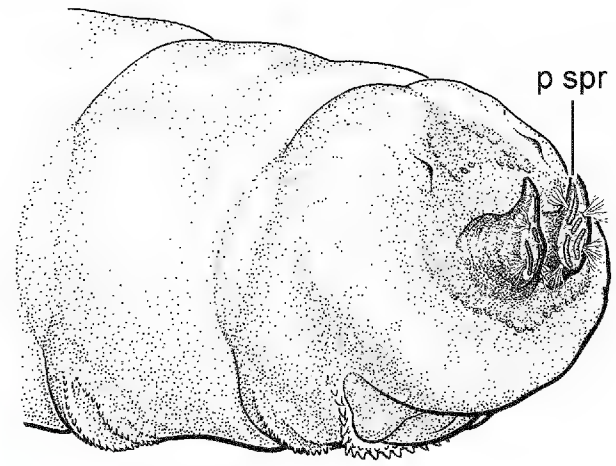


17 *Compsobata*

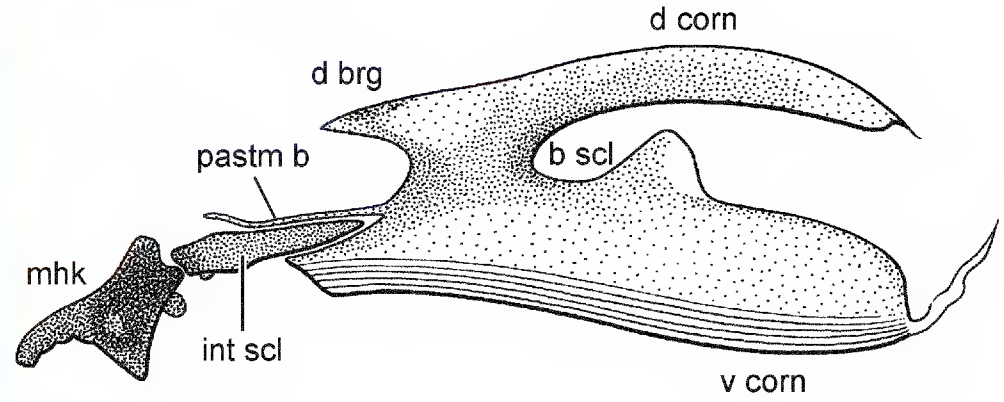
19 *Grallipeza*



20 *Grallipeza*



18 *Compsobata*



21 *Compsobata*

Figs 62.17–21. Immature stages of Micropezidae: (17) larval habitus of *Composobata univitta* (Walker), lateral view (non-Afrotropical); (18) same, posterior segments of larva, posterolateral view; (19) pupal habitus of *Grallipeza placidoides* Marshall, ventral view (non-Afrotropical); (20) same, anterior end of larva, lateral view; (21) cephaloskeleton of *C. univitta*, lateral view. Figs 17, 18, 21 (Steyskal 1987, figs 14, 16, 15, respectively).

Abbreviations: b scl – basal sclerite; d brg – dorsal bridge; d corn – dorsal cornu; int scl – intermediate sclerite; mhk – mouthhook; p spr – posterior spiracle; pastm b – parastomal bar; prth spr – prothoracic spiracle; v corn – ventral cornu.

that genus. Marshall (2019) recognised that it did not belong in *Cothornobata* and erected the monotypic genus *Paraeurybata*. *Paraeurybata taeniata* is the only Afrotropical representative of the subfamily Eurybatinae. Biology and immature stages remain unknown, but Marshall (2019) documented oviposition into beetle-borings in large fallen trees. The species was included in an identification key to Mascarene Micropezidae by Marshall (2019).

***Paramimegralla* Hennig** (Taeniapterinae)**.** An endemic genus of 18 species confined to Madagascar. Barraclough (1992*a*) divided the Malagasy micropezid fauna into *Mimegralla*, *Paramimegralla*, *Rainieria* and *Stiltissima* Barraclough, but a recent revision of the Micropezidae of Madagascar (Marshall 2017), treated the Malagasy species formerly in *Mimegralla* as *Hybobata* and treated all other Malagasy Micropezidae (18 species) as *Paramimegralla*. *Stiltissima* is a junior synonym of *Paramimegralla* and *Rainieria* does not occur in the Afrotropical Region. Biology and immature stages remain unknown. An identification key to all species was provided by Marshall (2017).

***Tanypomyia* Verbeke** (Taeniapterinae)**.** An endemic genus of two described species. *Tanypomyia* was described for *T. venusta* (Enderlein, 1922), from Cameroon, Democratic Republic of Congo, Equatorial Guinea and Uganda and *T. elegans* Verbeke, 1951, from Democratic Republic of Congo. Verbeke considered the Afrotropical endemic genera *Aristobatina*, *Cephalosphen*, *Erythromyiella*, *Glyphodera* and *Tanypomyia* to be closely related. Steyskal (1980: 581) treated *Tanypomyia* as part of *Mimegralla*, but it is probably most closely related to *Aristobatina* (Marshall 2014). Biology and immature stages remain unknown. Characters to distinguish the two species were provided by Verbeke (1951).

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NERIIDAE 63

(Neriid Flies or Cactus Flies)

Fernando da Silva Carvalho-Filho

Fig. 63.1. Male of *Chaetonerius* sp. (Tanzania) (photograph © S.A. Marshall).

Diagnosis

Small- to medium-sized (body length, including antennae: 5–15 mm), slender-bodied acalyptrate flies (Fig. 1), with long, stalk-like legs; body colour mostly brown or blackish brown, often with yellow markings.

Head usually longer than high, with eyes often dorsoventrally compressed (Figs 1–3); vibrissae absent in Afrotropical species; antenna porrect; antennal base (Fig. 3) present or absent; scape and pedicel elongate or short (invariably short in Afrotropical species) (Figs 2, 3), pedicel with narrow triangular apical process on inner side (Fig. 4); arista inserted apically, pubescent or bare (Figs 2, 3).

Thorax with wing membrane hyaline or fumose, sometimes darkened around the vein apices or along costal margin (Fig. 5); costal vein (*C*) thinned at subcostal vein (*Sc*), sometimes broken; veins R_{4+5} and M_1 convergent distally (Fig. 5). Legs long and slender, stilt-like (Fig. 1); fore coxa prominent, usually furnished with spine-like setae in males; male fore femur usually bearing row of anteroventral spine-like setae.

Abdomen with terminalia of both sexes elongated (Figs 6, 7); male terminalia flexed beneath abdomen, with epandrium long and narrow, with small apical surstylus and cercus (Fig. 7); female with segment 7 developed as long, sclerotised oviscape with bulbous base (Fig. 6).

Neriidae superficially resemble some species of Micropezidae (see Chapter 62) and Sciomyzidae (see Chapter 78), especially in body form and head shape. In Neriidae the arista is inserted apically and the pedicel has a triangular apical process on the inner side (Figs 2–4), while in Micropezidae and Sciomyzidae the arista is inserted dorsobasal and the inner side of the pedicel lacks an apical process.

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2021. Manual of Afrotropical Diptera. Volume 3. Brachycera—Cyclorrhapha, excluding Calyptratae. *Suricata* 8. South African National Biodiversity Institute, Pretoria; pp. 1517–1522.

Biology and immature stages

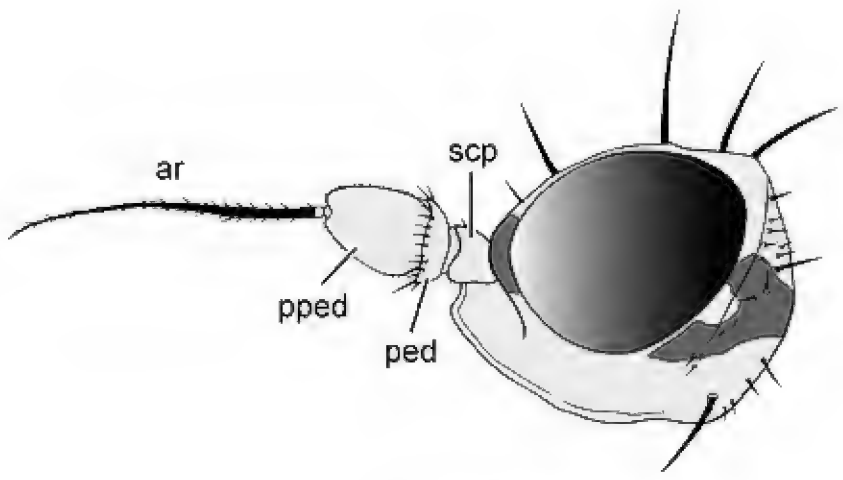
Little is known regarding the biology of Afrotropical neriid species, but at least two species of Afrotropical *Chaetonerius* Hendel have been bred from decaying pumpkin, *Cucurbita pepo* L. (Cucurbitaceae) (Barraclough 1993*a*).

Larvae of Neriidae, for which the biology is known, are basically saprophagous, occurring in a variety of decaying vegetable material, including decaying cambial tissue of dead and dying trees and rotting fruits (Berg 1947; Ferrar 1987: 251; Olsen & Ryckman 1963; Pitkin 1989). It has been suggested that larvae of some *Chaetonerius* species may be phytophagous (Barraclough 1993*a*).

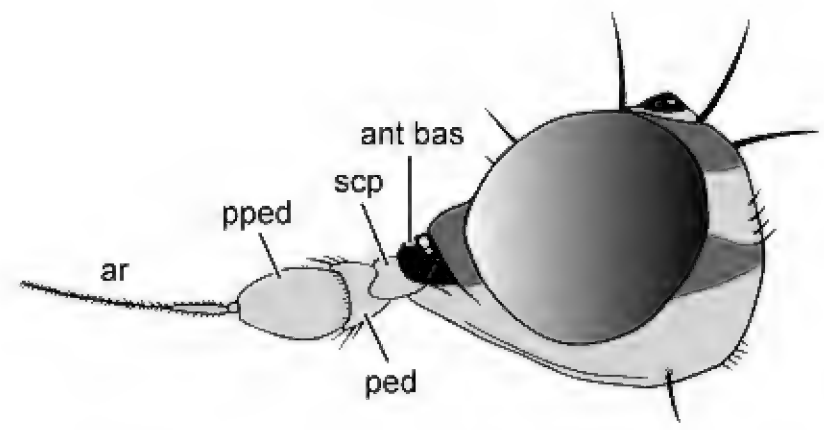
Females of a *Telostylinus* Enderlein species and the non-Afrotropical *Gymnonerius fuscus* (Wiedemann, 1824) were observed ovipositing in active beetle-borings in fallen trees in Asia (Preston-Mafham 2001). The egg, larva and puparium of the Nearctic species *Odontoloxozus longicornis* (Coquillett, 1904) and the Neotropical species *Glyphidops flavifrons* (Bigot, 1886) were described in detail by Olsen & Ryckman (1963) and Vinasco & Carrejo (2016), respectively. Steyskal (1965) provided additional information on the third-instar larva and puparium of *O. longicornis*. Larvae of *O. longicornis* were reared from rotting pockets of columnar cactus and rotting stems of papaya trees, *Carica papaya* L. (Caricaceae) (Olsen & Ryckman 1963; Steyskal 1965). The larva and puparium of *Telostylinus lineolatus* (Wiedemann, 1830) were described by Berg (1947), based on specimens found beneath the bark of papaya trees in Asia and the empty puparium was illustrated. The Neotropical species *Glyphidops pluricellatus* (Schiner, 1868) was bred from fruits of *Carludovica* sp. (Cyclanthaceae) (information from specimen labels) and *Glyphidops flavifrons* from rotting stems of papaya plants (Vinasco & Carrejo 2016). The immature stages of Afrotropical species have not yet been described.

Egg (Fig. 11) elongate, with longitudinal dorsal hatching seam and blunt posterior region; respiratory filament arising from anterior region, very long, more than 2 or 3 × longer than egg length, without respiratory filaments; chorion sculpted with many cells (Olsen & Ryckman 1963; Vinasco & Carrejo 2016). Larvae of Neriidae (Figs 8–10) are difficult to characterise and distinguish from other families having saprophagous larvae. The presence of four elliptic spiracular openings arranged along the periphery of the spiracular plate (Fig. 10) is, however, a fairly diagnostic feature (Foote 1991: 800). Vinasco & Carrejo (2016) also proposed as a diagnostic feature, the presence of the epipharyngeal sclerite and the labial sclerite.

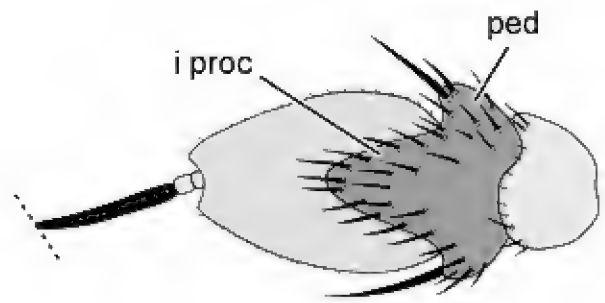
Neriid flies are usually encountered near larval food sources, where males of some taxa defend territories, with ritualised displays, fighting other males and engaging in aggressive confrontations (Bonduriansky 2006; Eberhard 1998; Preston-Mafham



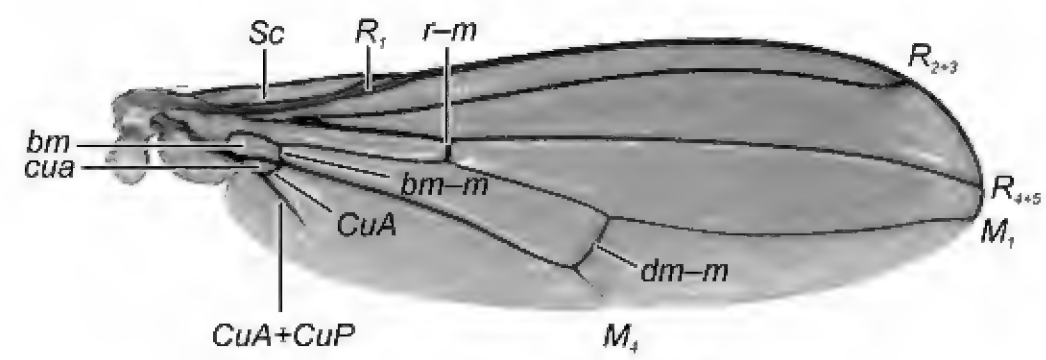
2 *Chaetonerius*



3 *Telostylinus*



4 *Chaetonerius*



5 *Chaetonerius*

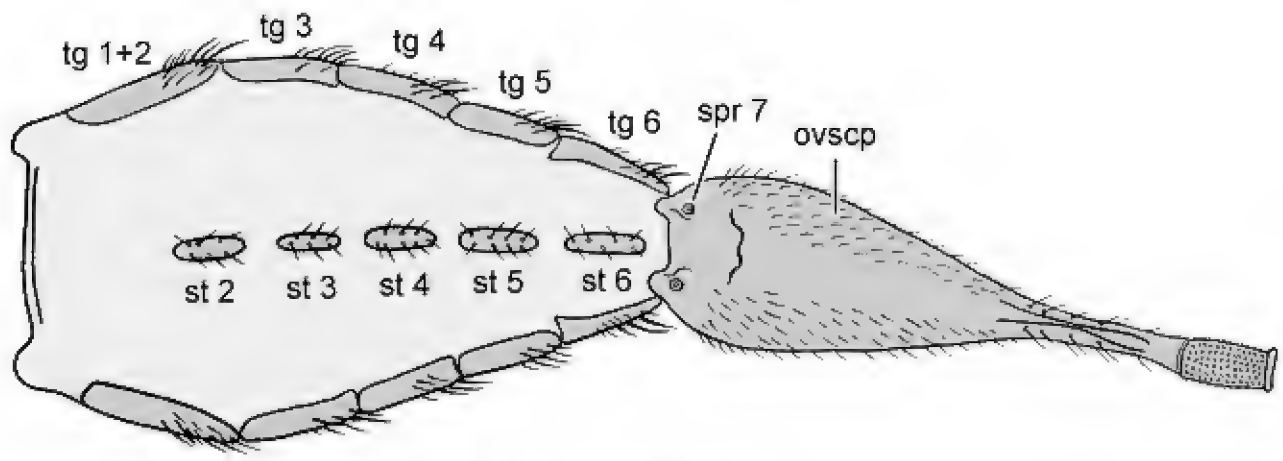
Figs 63.2–5. Heads, antenna and wing of Neriidae: (2) head of *Chaetonerius* sp., lateral view; (3) head of *Telostylinus* sp., lateral view; (4) antenna of *Chaetonerius* sp. (distal portion of arista omitted), medial view; (5) wing of *Chaetonerius* sp., dorsal view.

Abbreviations: ant bas – antennal base; ar – arista; *bm* – basal medial cell; *bm–m* – basal–medial crossvein; *CuA* – anterior branch of cubital vein; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *dm–m* – discal medial crossvein; i proc – inner process; M_1 – first branch of media; M_4 – fourth branch of media; ped – pedicel; pped – postpedicel; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Sc* – subcostal vein; scp – scape.

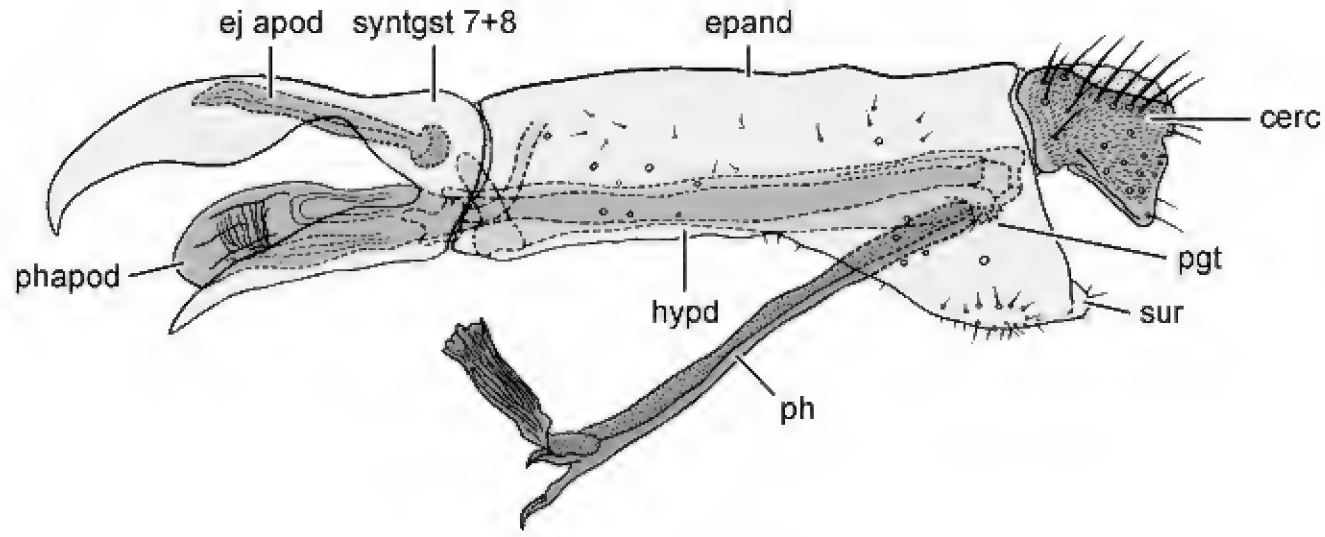
2001). In these fights, males usually raise their fore legs or the anterior portions of their bodies above the substrate, in some cases to an almost vertical posture and strike each other with their heads (Bonduriansky 2006; Eberhard 1998). Males also use their armed fore legs to slash one another (Eberhard 1998). Eberhard (1998) observed that male legs of Neotropical *Glyphidops flavifrons* (Bigot, 1886) sometimes become entangled, resulting in flies falling on their heads on the substrate.

Males exhibit little or no precopulatory courtship displays (Bonduriansky 2006; Eberhard 1998), although males of Neotropical *Nerius plurivitatus* Bigot, 1886 and *N. pilifer* F., 1805 have been observed to "dance" in large arcs in front of females, while opening and closing their wings (Carvalho-Filho, unpubl.; Eberhard 1998). Mate guarding during oviposition has been recorded for males of many species, where they enclose the females within the span of their legs (Bonduriansky 2006; Eberhard 1998; Preston-Mafham 2001).

Some species may be attracted to decaying vegetable matter and some have been collected on the dung and droppings of both large (elephant) (Barraclough 1993*a*) and small (gecko) (Carvalho-Filho, unpubl.) vertebrates. Adults were obtained from hanging traps baited with fermenting fruit-baits both in Sulawasi and in central and southern Africa (A.H. Kirk-Spriggs, pers. comm. 2014). Adults of Oriental *Telostylinus lineolatus* (Wiedemann, 1830) have been frequently found alighting on decaying pig carcasses in Malaysia (Chin *et al*. 2011) and adults of *Nerius* F. and *Glyphidops* Enderlein spp. have been collected in traps baited with rotting beef lung in the Brazilian Amazon (Carvalho-Filho, unpubl.). These substrates are not used as oviposition sites, however, as larvae were not found in pig carcasses (Chin *et al*. 2011) or in beef lung (Carvalho-Filho, unpubl.). The odour emanated from the scars of a dying large tree, on which females of *Nerius pilifer* were ovipositing, is similar (at least to a human observer) to that of rotting beef lung bait (Carvalho-Filho, unpubl.). Adults of some *Chaetonerius* and *Telostylinus* species have been found in dense flowers, including bananas (Shimelash *et al*. 2008) and Torch ginger, *Etlingera elatior* (Jack) R.M. Smith (Zingiberaceae) (Carvalho-Filho, unpubl.) and a *Glyphidops* species was reared from an arum flower, *Dieffenbachia* sp. (Araceae) (Carvalho-Filho, unpubl.). Thus, neriids probably seek dense flowers as oviposition sites, rather than as a source of pollen or nectar. Some adults of different species have also been observed "licking" tree exudates and fluids of rotting animal matter (Carvalho-Filho, unpubl.; Chin *et al*. 2011), with females usually "licking" the substrate prior to oviposition (Eberhard 1998; Preston-Mafham 2001).



6 *Chaetonerius* ♀



7 *Chaetonerius* ♂

Figs 63.6–7. Abdomen and terminalia of Neriidae: (6) female tergites, sternites and oviscape of *Chaetonerius* sp., ventral view; (7) same male terminalia, lateral view.

Abbreviations: cerc – cercus; ej apod – ejaculatory apodeme; epand – epandrium; hypd – hypandrium; ovscp – oviscape; pgt – postgonite; ph – phallus; phapod – phallapodeme; spr – spiracle; st – sternite; sur – surstylus; syntgst – syntergosternite; tg – tergite.

Many neriid flies occur in shaded situations in humid primary and secondary forests, although some *Chaetonerius* species have been collected in dry habitats, including suburban areas in southern Africa (Barraclough 1993*a*). Adults of some species frequently sit on the stems of large trees in a characteristic head-downwards position (Barraclough 1993*a*; Carvalho-Filho, unpubl.).

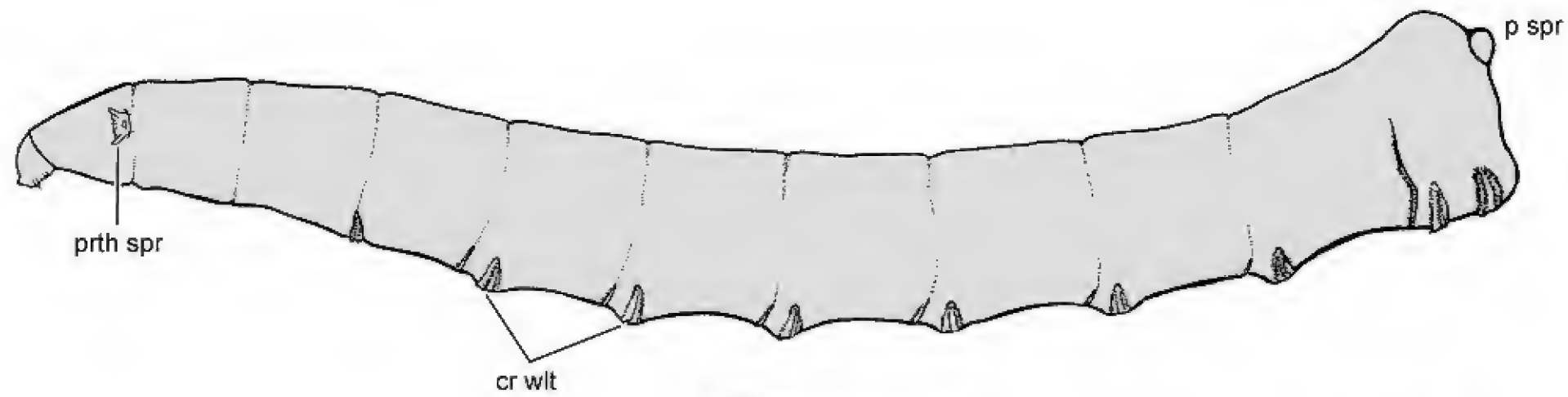
Economic significance

Although neriid flies do not have any known appreciable economic impact, Evans (2008) pointed out that *Chaetonerius latifemur* Enderlein, 1922, is a potential vector of plant pathogens, such as the fungus-like eukaryotic *Phytophthora palmivora* Butler (Pythiaceae), that causes Black pod disease of Cacao, *Theobroma cacao* L. (Malvaceae) in Ghana.

Classification

The family Neriidae is assumed to be a monophyletic group in the superfamily Nerioidea, that also includes the non-Afrotropical family Cypselosomatidae and Micropezidae (Koch *et al.* 2015; Pape *et al.* 2011). Neriidae was initially considered to be a subfamily of Micropezidae (Aczél 1949; Enderlein 1922; Hennig 1936), but has been treated as a full family by most authors, including all recent authors since Aczél (1951). This family was once considered to be most closely related to Micropezidae (Griffiths 1972: 160–161), but according to the phylogenetic hypotheses shown by McAlpine (1989: 1431) and Wiegmann *et al.* (2011) Micropezidae is the sister-group of the clade composing Neriidae and non-Afrotropical Cypselosomatidae.

Neriidae comprises *ca* 112 species in 19 genera (Pape *et al.* 2011) and is predominately circumtropical in distribution. The family is most abundant in the Neotropical Region, with species there accounting for one-third of the described fauna. Aczél (1954*b*) proposed the division of the family into two subfamilies: Neriinae and Telostylinae, although such a formal subfamilial division of Neriidae remains contentious and this arrangement has not been adopted by some authors (Barraclough 1993*a*; Buck 2010; Pitkin 1989). Neriinae is assumed to be monophyletic and is characterised by the swollen and medially divided upper face forming the antennal base (antennal socket) just below the ptilinal fissure (Aczél 1954*b*; Buck 2010). Telostylinae, on the other hand, is believed to be an unnatural assemblage of species (Buck 2010). Koch *et al.* (2015) provided



Figs 63.8–11. Third-instar larva and egg of Neriidae: (8) third-instar larva of *Odontoloxozus longicornis* (Coquillett), lateral view (non-Afrotropical); (9) same, cephaloskeleton, lateral view; (10) same, posterior spiracle, dorsal view; (11) same, habitus of egg, lateral view. Figs 8, 10–11 (after Olsen & Ryckman 1963, figs 1, 2, 8), Fig. 9 (after Steyskal 1965, fig. B).

Abbreviations: cib – cibarium; cr wlt – creeping welts; d brg – dorsal bridge; d corn – dorsal cornu; ecdys sc – ecdysial scar; int scl – intermediate sclerite; mhk – mouthhook; p spr – posterior spiracle; prth spr – prothoracic spiracle; pstig tft – peristigmatic tuft; spr o – spiracular opening; v corn – ventral cornu.

the first comprehensive phylogenetic analysis of Neriidae based on morphological characters and the subfamilies were not recovered as monophyletic. Koch *et al.* (2015), however, did not propose a higher-level taxonomic division of the family. Therefore, the subfamilial division is not utilised in this chapter.

Identification

The Afrotropical fauna is essentially composed of a single genus, *Chaetonerius*. An undetermined invasive species of *Telostylinus* has been recorded from some western Indian Ocean islands of the Afrotropical Region (Barraclough 1992).

Specific determinations of Afrotropical species of Neriidae are made using external characters, such as wing markings, male fore femur vestiture, leg colour and head patterning. Unlike many other Neriidae genera, the shape of male terminalia is also an important character in determining species in *Chaetonerius* (Barraclough 1993a). Neriidae are best director micro-pinned in the field for later double-mounting (see Chapter 2).

Key to the genera of Afrotropical Neriidae

1. Thorax with 2 notopleural setae; head without antennal base (antennal socket) (Fig. 2); fore coxa bearing spine-like setae in males. . . . . .*Chaetonerius* Hendel
– Thorax with 1 notopleural seta; head with antennal base prominently exposed (Fig. 3); fore coxa without spine-like setae in males . . . . . *Telostylinus* Enderlein

Synopsis of the fauna

***Chaetonerius* Hendel.** Occurring in tropical areas of the Oriental and Afrotropical Regions, with one species reaching the Australasian Region (Barraclough 1993*a*; Pitkin 1989). There are about 20 described species, 15 of which are recorded from the Afrotropical Region (Barraclough 1993*a*). The majority of species occur in equatorial and sub-equatorial Africa, with few records for Southern Africa; one species, *C. alluaudi* (Giglio-Tos, 1895), was recorded from Madagascar, Mauritius and Seychelles in the Indian Ocean (Barraclough 1993*a*, *b*; Steyskal 1980: 578). Aczél (1954*a*) provided an identification key to the then known Afrotropical species, but this work should be used with caution, as it employs variable characters, such as femoral colour and needs to be supplemented by the addition of new species and taxonomic arrangements (Barraclough 1993*a*, *b*). Southern African species were keyed by Barraclough (1993*a*).

***Telostylinus* Enderlein.** This genus is predominately Australasian and Oriental in distribution and includes about 19 species. The only (unidentified) Afrotropical species, recorded from Seychelles, is assumed to represent an introduction (Barraclough 1992).

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DIOPSIDAE 64

(Stalk-eyed Flies and Afromontane Forest Flies)

Hans R. Feijen and Cobi Feijen

Fig. 64.1. Male of *Diopsis surcoufi* Séguy (Tanzania) (photograph © S.A. Marshall).

Diagnosis

Small- to medium-sized acalyptrate flies (body length: 3–13 mm; eye span in stalk-eyed species: 1.5–19 mm) (Figs 1, 4); slender-bodied, more compact-bodied in small species; colouration variable, most commonly blackish, greyish or black with chestnut brown, more rarely yellowish brown; setulose species uncommon; species-specific pruinescence patterns commonly on thorax and/or abdomen; head with lateral projections (stalks) bearing compound eyes apically, antennae subapically (Figs 1, 4–7); scutellum with 2 posterior elongations; Centrioncinae without stalks, but with rounded head (Figs 2, 3).

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2021. Manual of Afrotropical Diptera. Volume 3. Brachycera—Cyclorrhapha, excluding Calyptratae. *Suricata* 8. South African National Biodiversity Institute, Pretoria; pp. 1523–1543.

Head markedly with dichoptic eyes in stalk-eyed subfamilies, but Centrioncinae also dichoptic; usually with 2 pairs of sometimes spinous setae (Figs 2, 4, 12), in Centrioncinae considered as one pair of fronto-orbital setae and one pair of outer vertical setae, in the stalk-eyed species usually named inner and outer vertical setae; antenna with 3-articled arista in Centrioncinae and Sphyracephalinae, 2-articled in Diopsinae, pubescent in Centrioncinae (Figs 2, 3), bare or basally slightly microtrichose in stalk-eyed species; pedicel without dorsal lobes, but with distal conus inserted into basal hollow of postpedicel; postpedicel ventrally extended in Centrioncinae (Figs 2, 3); ocelli on raised tubercle.

Thorax with large, collar-like pronotum in stalk-eyed species, pronotum short in Centrioncinae; stalkless flies with lanceolate basiliform prosternum (Fig. 13), stalk-eyed species with square, basiliform prosternum (Fig. 14) or prosternum fused laterally with proepisternum forming precoxal bridge (Fig. 15); postpronotum well-defined, rounded to elongate; scutum (Figs 8–11), usually with 0–3 pairs of setae (presutural, supra-alar and intra-alar setae), rarely dorsocentral and acrostichal setae present; all stalk-eyed species (not Centrioncinae), with pleurotergal spines (Figs 8–9), two Oriental genera with supra-alar spines and one Afrotropical genus with intra-alar spines. Scutellum with 2 posterior elongations, varying from small protuberances with long apical scutellar setae, to strong spines without setae (Figs 1–4, 9). Wing (Figs 16–28) slender, microtrichia covering varying from almost uniform to less than distal ½; alula present in Centrioncinae (Fig. 16) and Sphyracephalinae (Figs 18, 27), absent in Diopsinae (Figs 17, 19, 20–26, 28); costal vein (C) without breaks (Fig. 16); cells *bm* and *dm* confluent (Fig. 16); position of former crossvein *bm–m* often indicated; vein *CuA+CuP* reaching wing margin in Centrioncinae (Fig. 16), extending beyond cell *cua* in Sphyracephalinae (Figs 18, 27), absent in Diopsinae (Figs 17, 19, 20–26, 28); vein M_4 reaching wing margin in Centrioncinae (Fig. 16) and *Diopsis* L. (Figs 21–24), not reaching margin, but extending beyond cell *bm+dm* in most other diopsids (Figs 17–20, 25–28); wing pattern variable, hyaline to infuscated, with central, preapical or apical maculae, or brownish to dark and irrorated with 3 bands of transparent maculae. Legs with fore femur often incrassate (Figs 1–4), ventrally with double row of tubercles (Figs 30, 31), in some taxa bordered by rows of spinous setae (Fig. 30); hind femur only in Centrioncinae with tubercles (Fig. 29).

Abdomen (Figs 32–37) varying from relatively long and slender, to short and strongly clavate; syntergite 1–2 in Centrioncinae and Sphyracephalinae, syntergite 1–3 (rarely 1–4) in Diopsinae; male terminalia in Centrioncinae with massive inverted sternite 8, fused to sternite 7 forming complete ventral band of sclerotisation (Fig. 38), in stalk-eyed diopsids a slender, dorsal syntergosternite 7 + 8 (Figs 39–41); surstylus trilobed, articulated in Centrioncinae (Figs 46, 47), in stalk-eyed species articulating or fused with epandrium, relatively simple (Figs 48–50), with at most, an apophysis; phallapodeme small, with posterior ⅔ fused to hypandrium (Centrioncinae) or large, linked to hypandrium *via* lateral processes; phallus just larger than complex of hypandrium/phallapodeme (Centrioncinae), or < ½ size of complex (stalk-eyed species), phallus a single, solid structure, with complex distal section (Centrioncinae) or open, complex, with delicate structure of various sclerites and stylets basally linked to a ring formed by basiphallus (stalk-eyed species); ejaculatory apodeme present; female terminalia (Fig. 51), with 3 (2 + 1) spermathecae present, except for *Diasemopsis* Rondani genus-group with 2 (1 + 1) spermathecae.

Egg elongate, with chorion striate in Centrioncinae and Diopsinae (Fig. 52), reticulated in Sphyracephalinae. Larva fusiform, tapering anteriorly, blunter posteriorly (Fig. 56), with elaborately ornamented, often species-specific, prothoracic (Figs 53, 54, 57) and posterior spiracles (Fig. 55); cephaloskeleton (Figs 53, 58), with paired mouthhooks of simple, curved form. Puparium elongate, sub-cylindrical (Fig. 59), with anterior and posterior spiracular stalks.

Adult stalk-eyed species of Diopsidae are unmistakable, with their eyes and antennae born at the end of stalks, although the stalk-eyed condition occurs convergently in at least eight other families of Diptera, notably in the Clusiidae (see Chapter 81), Platystomatidae (see Chapter 70), Tephritidae (see Chapter 71) and Ulidiidae (see Chapter 69). In the Afrotropical Region the condition is most pronounced in the platystomatid genera *Agrochira* Enderlein and to a lesser degree in *Mesanopin* Enderlein and in the tephritid genus *Themarictera* Hendel. Only in the Diopsidae are the antennae also located on the stalks. Centrioncinae are more difficult to distinguish and look superficially similar to other slender acalyptrate flies. These stalkless Diopsidae can be recognised by the incrassate fore femora, with rows of tubercles and spinous setae, by the tiny tubercles on the hind femora and by the posterior protuberances of the scutellum. In the Centrioncinae, which occur in forest situations, the typical forwardly directed testing movements of the fore legs ("air treading") are also a good indication of identity.

Biology and immature stages

For the Centrioncinae, some ecological aspects were discussed by Feijen (1983). They are univoltine, beginning reproduction towards the end of the dry season and can lay up to 50 eggs. The biology of the larvae of this subfamily remains unknown.

The lifecycle of Sphyracephalinae has been relatively well-studied (Descamps 1957: 121; Hochberg Stasny 1985; Lavigne 1962; Sen 1921). Afrotropical species prefer a wet, rocky environment, with some moss covering and the larvae are saprophagous. At least Nearctic species are known to congregate towards evening (Hochberg Stasny 1985), while these flies also congregate at hibernation sites. In the Afrotropical Region, aestivation was described by Feijen (1984), who found, in Malawi, a cluster of around 100,000 specimens in an area of less than 0.2 m^2. Clustering in stalk-eyed flies was reviewed by Feijen *et al*. (2017). Nothing is known about the biology of *Cladodiopsis* Séguy.

Afrotropical Diopsinae occur in shady humid habitats, along margins of streams and pools, in rainforests and in marshy areas. Ecologically, they can be divided into savanna-inhabiting (more open terrain) diopsids and rainforest-inhabiting diopsids. Savanna species disperse during the rainy season over the plains, but concentrate in the dry season along wet places with some shade. Dense aggregations can number thousands of flies and may include 10–20 species (Feijen *et al*. 2017). Savanna flies can move to higher elevations in the dry season, but

only some species then enter montane forests. The rice stem-borer, *Diopsis longicornis* Macquart, 1835, can move up to 20 km away from paddy fields with an elevational migration of > 1,000 m. Rainforest diopsids spend the dry season along forest streams and disperse in the rainy season. The larvae of most species of Diopsinae are saprophagous, but in a few Afrotropical *Diopsis* larvae are obligatory phytophagous stem-borers of Poaceae (Descamps 1957: 114; Feijen 1989: 42). Larvae of a larger group of *Diopsis* act as secondary stem-borers, feeding on frass of lepidopterous borers and even turning predatory

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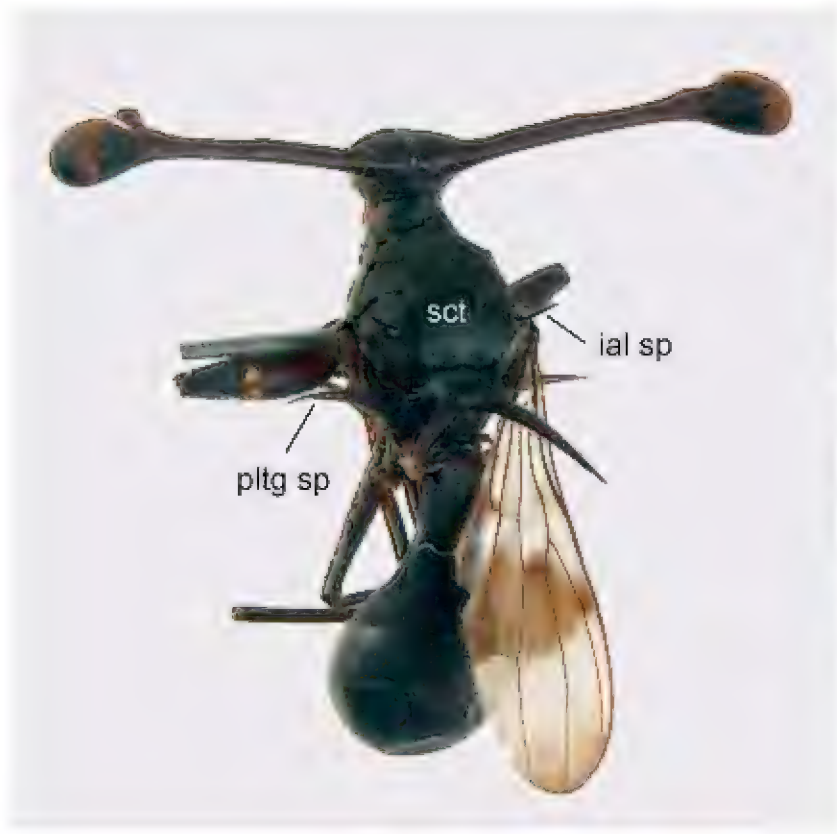
Figs 64.2–7. Living examples of Afrotropical Diopsidae: (2) *Centrioncus decoronotus* Feijen (Kenya); (3) copulating pair of *Teloglabrus sanorum* Feijen (South Africa); (4) *Sphyracephala beccarii* (Rondani) (Tanzania); (5) *Cladodiopsis seyrigi* Séguy (Madagascar); (6) copulating pair of *Madagopsina apollo* (Brunetti) (Madagascar); (7) *Gracilopsina sinespina* Feijen, Feijen & Feijen (Madagascar). Fig. 2 (photograph © D. Gavryushin), Figs 3–5 (photographs © S.A. Marshall), Fig. 6 (photograph © R. Krekels), Fig. 7 (Feijen *et al*. 2018, fig. 3).

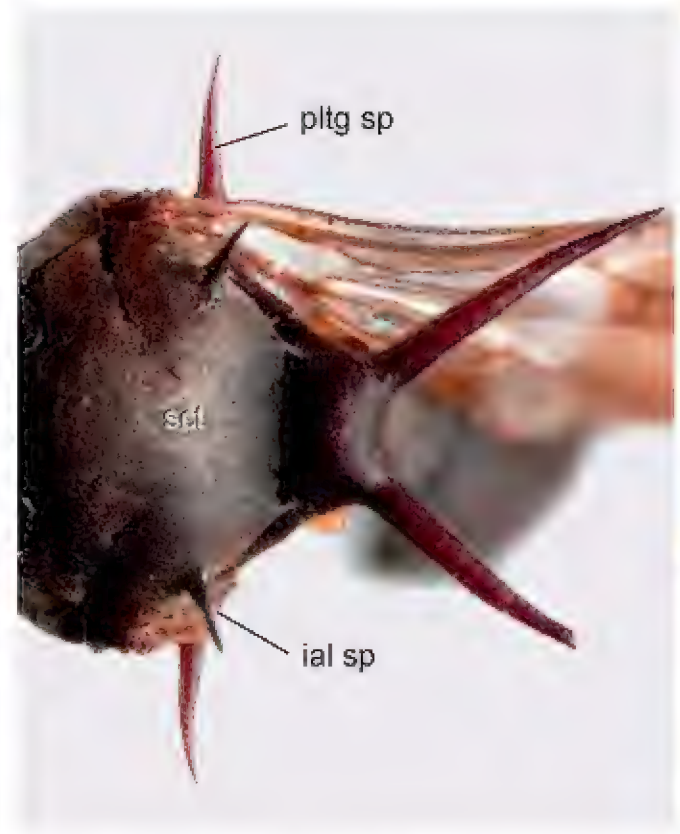
and cannibalistic. Larvae of saprophagous species pupariate in more or less rotting material. The stem-boring *Diopsis*, however, needs to pupariate in the leaf sheaths of the stem, otherwise the puparium may warp and the pharate adult is unable to eclose.

Phytophagous species usually adhere their eggs one by one onto the host-plant. Descamps (1957: 28), however, mentioned several species oviposit eggs in clusters. In the female of an undescribed *Diopsis* species from Democratic Republic of Congo and Kenya, the distal abdominal tergites and cerci are laterally compressed and strongly sclerotised. This stiff, sharp abdominal tip likely serves to penetrate the host-plant prior to oviposition. Descamps (1957: 124) and Morgan & Abu (1973) recorded 2–3 generations per year for *D. longicornis* in West Africa, although in Southern and East Africa the same species was found to be univoltine, with perhaps a minor second generation (or later reproducing section of the same generation) occurring in the dry season (Feijen 1989: 38). The difference could be linked to the cropping system (2–3 *versus* 1 or 2 crops per year). Chiasson & Hill (1995), recorded only one generation in a single crop system in Guinea and discussed the dormancy pattern. Descamps postulated for Cameroon up to eight generations in some *Diasemopsis* and *Diopsis*, but in East Africa, Malawi and Mozambique these genera are, as a rule, univoltine. The Asian genera *Cyrtodiopsis* Frey and *Teleopsis* Rondani are polyvoltine (Motte & Burkhardt 1983; Wilkinson 1993). Diopsidae are long-lived: univoltine species live up to one year, while Burkhardt & Motte (1983*a*) recorded a life span of one and a half years for an Asian species.

For the morphology of egg, larva and puparium of Diopsidae (Figs 52–59), the reader is referred to Descamps (1957: 33), Feijen (1989: 31), Feijen *et al*. (2018), Ferrar (1987: 141),

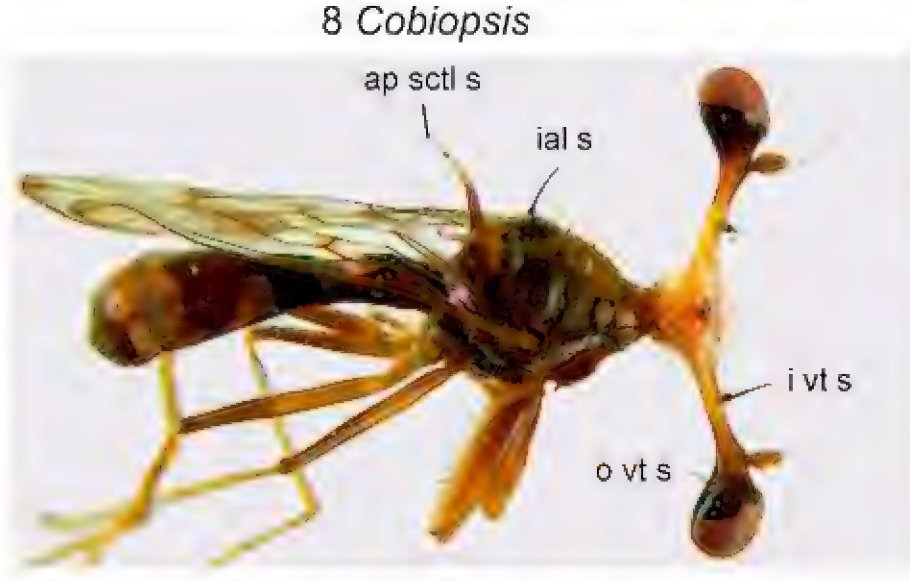


8 *Cobiopsis*



9 *Cobiopsis*

10 *Diasemopsis*



11 *Trichodiopsis*

12 *Trichodiopsis*

Figs 64.8–12. Habitus, thorax and head of Diopsidae: (8) habitus of *Cobiopsis latifascia* (Brunetti), dorsal view ♂; (9) same, scutal and scutellar spines; (10) thorax of *Diasemopsis aethiopica* (Rondani), dorsal view ♀; (11) habitus of *Trichodiopsis pulchella* (Eggers), dorsolateral view ♀; (12) same, head, anterior view.

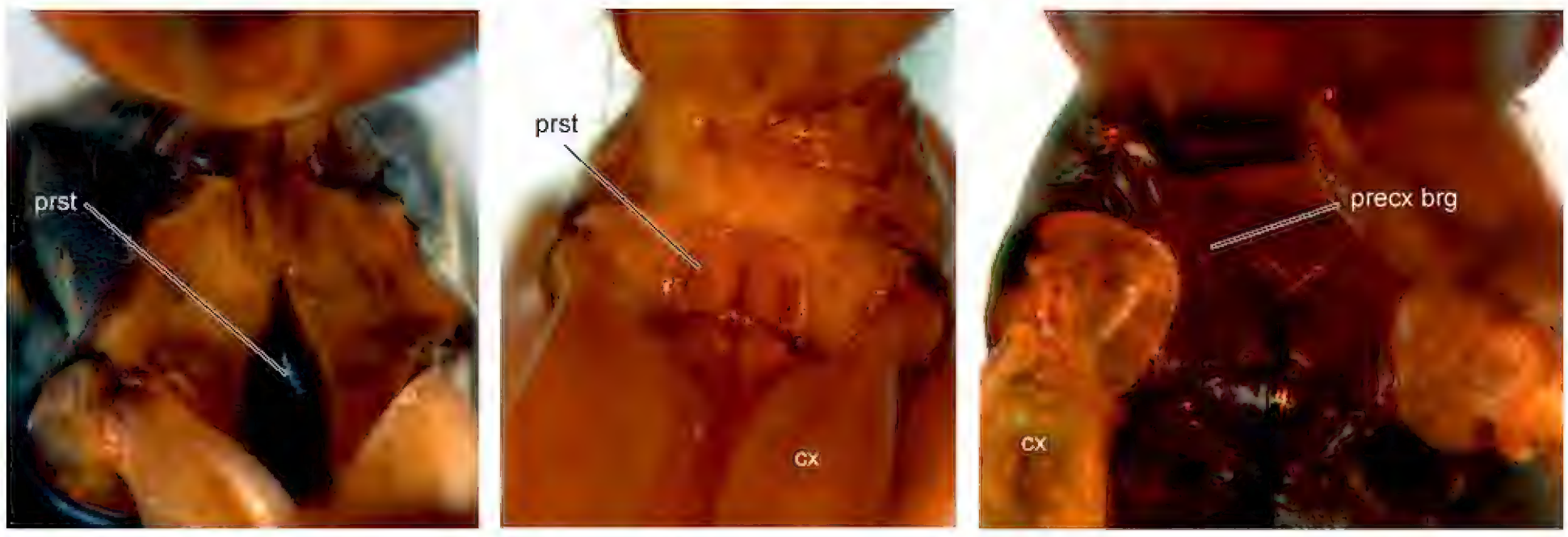
Abbreviations: ap sctl s – apical scutellar seta; i vt s – inner vertical seta; ial s – intra-alar seta; ial sp – intra-alar spine; o vt s – outer vertical seta; pltg sp – pleurotergal spine; sct – scutum.

Hochberg Stasny (1985), Lavigne (1962), Meier & Hilger (2000) and Sen (1921). In the Afrotropics, research on Diopsidae has concentrated on the ecology of the rice stem-borers (Cochereau 1978; Descamps 1957: 93; Feijen 1979, 1984; Scheibelreiter 1974), but Descamps (1957: 151) already considered sexual dimorphy with regard to eye span. Information on arthropod predators can be found in Descamps (1957: 144) and Feijen (1984: 21), while the ecology of hymenopterous parasitoids of Diopsidae was discussed by Feijen (1984: 24) and Feijen & Schulten (1981). A single case of predation by a bird was mentioned by Oatley (1970).

The relation between Diopsidae and Laboulbeniales (Ascomycota – sac fungi) deserves special mention. Laboulbeniales are very common on Afrotropical Diopsidae, considerably less common on Oriental Diopsidae and are not known from the extant Holarctic Sphyracephalinae. To date, 26 species of Laboulbeniales have been described from Diopsidae (Feijen 1989: 39; Rossi 1990*a*, *b*; Rossi & Feijen 2018). These fungal parasites are distributed over three genera: 3 *Laboulbenia* Montagne & Robin, 10 *Stigmatomyces* Karsten and 13 *Rhizomyces* Thaxter. In Malawi, representatives of all three genera were occasionally found on the same diopsid specimen. The only fossil Laboulbeniales known, *Stigmatomyces succini* Rossi, Kotrba & Triebel, was found in Baltic Amber on the diopsid *Prosphyracephala succini* (Loew, 1873) (Rossi *et al*. 2005). Three reasons can be given for the prevalence of Laboulbeniales on Diopsidae: (1) they occur in humid conditions, such as rainforests, wet habitats in savannas and along rivers; (2) they exhibit gregarious behaviour; and (3) they are long-lived as adults (in the Afrotropics, species are mostly univoltine with a life span of around a year). In addition, due to a shift from earlier to later reproducing flies, an overlap occurs between generations (Rossi & Feijen 2018). During the life span of Afrotropical diopsids the percentage of parasitism increases and can, in a species like *Diopsis longicornis*, almost reach 100%, especially in males. Frequency distributions of the fungal parasites on Afrotropical diopsids form a powerful argument for the univoltine nature of these flies. In Asia, species from *Cyrtodiopsis*, *Megalabops* Frey and *Teleopsis* are often polyvoltine and have a relatively short life span. Rossi & Feijen (2018: 10) indicated that "… the short lifespan appears to form the key factor", why Laboulbeniales are relatively uncommon in these genera. It should be noted that for some Afrotropical univoltine species and species-groups, like the *Diopsis circularis* species-group and the *Diopsis gnu* and *Diopsis carbonaria* species-groups, Laboulbeniales are very rare or unknown.

Rhizomyces species are only known from Afrotropical Diopsidae. They are found on *Centrioncus* Speiser, *Chaetodiopsis* Séguy, *Cobiopsis* Feijen, *Diasemopsis*, *Diopsina* Curran, *Diopsis* and *Teloglabrus* Feijen. It appears that representatives of *Rhizomyces* are more common on Centrioncinae and on the *Diasemopsis* genus-group (*Diasemopsis*, *Cobiopsis* and *Chaetodiopsis*), than on *Diopsina* and *Diopsis*. Moreover, the two groups of diopsids are also parasitised by two different species-groups of *Rhizomyces*. Although several of the very common *Diasemopsis* species, such as *Diasemopsis aethiopica* (Rondani, 1873) and *Diopsis* species, such as *Diopsis cruciata* Curran, 1934, occur in large mixed groups for more than half of the year, there is absolutely no exchange of *Rhizomyces* parasites belonging to the two different groups. In *Diopsis*, representatives of *Laboulbenia* and *Stigmatomyces* are much more common than those of *Rhizomyces*. *Rhizomyces* have never been encountered on Afrotropical *Sphyracephala* Say.

In Asia, initial research on the biology of diopsids by Frey (1928), Sen (1921) and Tan (1965) was greatly expanded by a series of publications by Burkhardt & Motte (1987, 1988), in which they studied the behaviour and the importance of eye stalks in sexually dimorphic species. At lekking/sleeping places, larger males defend harems of females. In ritualised fights, eye stalks indicate the size and strength of an individual and males with a larger eye span have an increased probability of



13 *Centrioncus* 14 *Madagopsina* 15 *Gracilopsina*

Figs 64.13–15. Thoracic features of Diopsidae (ventral views): (13) basiliform prosternum of *Centrioncus* sp. ♀; (14) same, *Madagopsina apollo* (Brunetti) ♂; (15) precoxal bridge of *Gracilopsina vadoni* (Vanschuytbroeck) ♂. Figs 14, 15 (Feijen *et al*. 2018, figs 4, 5).

Abbreviations: cx – coxa; precx brg – precoxal bridge; prst – prosternum.

reproduction. Burkhardt & Motte (1983*b*) also stressed the selective advantage of eye stalks in both sexes in providing better spatial vision. Various other theories for the functions of eye stalks were discussed by Burkhardt & Motte (1996: 172) and Feijen (1989: 50). In the past 30 years, studies of the biology of Diopsidae multiplied, also stimulated by the establishment of laboratory cultures. Major advances were made in the fields of genetics, morphology, ethology, physiology, evolution and molecular biology. The functions of the (often sexually dimorphic) eye stalks and sexual selection form a central axis in these studies. For introduction on these studies the reader is referred to Baker & Wilkinson (2001, 2003), Carr (2008), Christianson *et al*. (2005), Cotton *et al*. (2006), David *et al*. (2000), Lande & Wilkinson (1999), Swallow *et al*. (2005), Warren & Smith (2007), Wilkinson & Dodson (1997: 310) and Wilkinson *et al*. (1998, 2003, 2005). As a result, Diopsidae turned into model organisms, especially in the field of ornamental sexual traits. The sexually selective advantage of longer eye stalks has now been well-established for the dimorphic species, but also given the large number of monomorphic species, other selective advantages require additional study. Worthington & Swallow (2011), stated that relatively little is known about how diopsids avoid and deter predators. Their results suggested a strong sex difference in anti-predatory behaviour. Feijen (1989: 52), described the habit, especially of *Diopsis* species on Poaceae, of immediately switching to the reverse side of narrow leaves when disturbed. One or both eyes are then protruding from behind the leaf. Feijen (1984) briefly discussed the phenomenon that the average eye span in *D. longicornis* fluctuates during the year. In young flies, a selection against shorter eye span occurs, leading to an increase in the average eye span. The reverse occurs in older flies when the reproductive phase begins. Feijen & Feijen (2009) stated that in various *Diopsis*, ecological selection pressure on eye span may play an important role next to sexual selection. In this regard, they indicated that in *D. longicornis* the mean ratio eye span/body length amounted to 1.29 in females against 1.49 in males. In Asian diopsids, on which most of the work on sexual selection processes was undertaken, this ratio never goes above 1.0 for females. Eye stalks also play a role in assertive behaviour on food sites and in interspecific encounters.

For the rate of dimorphism (D), the difference between males and females in allometric slope for eye span on body length is commonly used: a brief review is provided by Feijen & Feijen (2009). The categories of monomorphy/dimorphy distinguished are given in Feijen *et al*. (2018). For monomorphy $D < 0.25$ is used. Very high dimorphy ($D > 3$) only occurs in the Oriental genus *Teleopsis*. Monomorphy or levels of dimorphy are clearly linked to genus- and species-groups. In the more early branching Sphyracephalinae, *Sphyracephala* shows homomorphy to low dimorphy, while *Cladodiopsis* has moderate to high dimorphy. In the *Diasemopsis* genus-group, *Cobiopsis*, *Chaetodiopsis* and *Diasemopsis* are all dimorphic, but the species of *Trichodiopsis* Séguy show homomorphy or low dimorphy. In the three Afrotropical genera belonging to the "irrorated wing" clade (see Feijen *et al*. 2018), *Diopsina* is monomorphic, *Madagopsina* Feijen, Feijen & Feijen has low to moderate dimorphy and *Gracilopsina* Feijen, Feijen & Feijen moderate to high dimorphy. In *Diopsis*, the situation is diverse: the species of three large species-groups are all monomorphic, while the species of three other large species-groups all exhibit low to moderate dimorphy. Baker & Wilkinson (2001: 1373), comparing allometric data with a phylogenetic tree, concluded that for the Diopsidae "Sexual dimorphism in eye span has evolved independently at least four times in the family ...". Feijen & Feijen (2020) increased the number of cases of independent development of sexual dimorphism with regard to eye span to ten.

Feijen (1989: 54) and Wilkinson & Dodson (1997: 318), indicated that apparent reversed sexual dimorphism for eye span (females having a longer eye span than males) in *Sphyracephala brevicornis* (Say, 1817) is due to females being larger overall, while no difference could be found in eye span/body length regressions. Feijen & Feijen (2009), however, found that in several Afrotropical *Diopsis*, eye span, in absolute and relative terms, was slightly longer in females than in males. Some *Diopsis* species have negative Ds varying from -0.2 to -0.7.

Economic significance

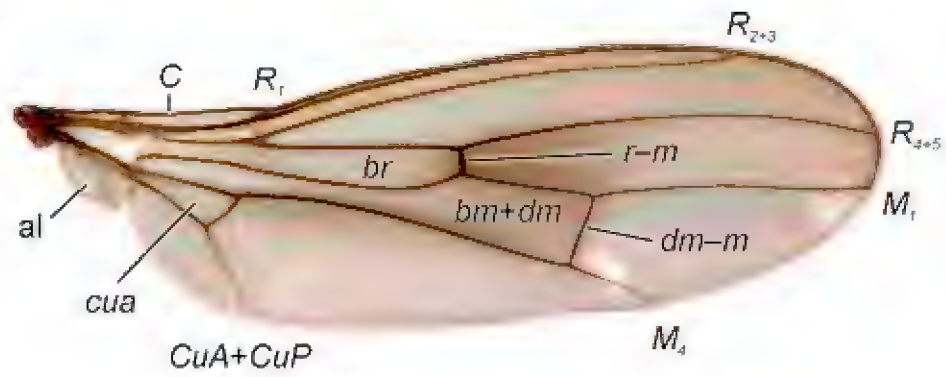
Mally (1920) was the first to record *Diopsis mayae* Feijen & Feijen, 2017 (as *D. apicalis* Dalman, 1817) as a secondary stem-borer of Maize, *Zea mays* L. (Poaceae) in South Africa, while Risbec (1947, 1950: 152) mentioned several *Diopsis* species as rice stem-borers in West Africa. Descamps (1957: 114) recorded *D. longicornis* (as *D. thoracica* Westwood, 1835) as a major pest of cultivated rice, *Oryza* spp. (Poaceae), and publications dealing with *D. longicornis* (often as *Diopsis macrophthalma*, which represents the genus *Diasemopsis* (Feijen 1987: 410)) increased from the 1960s to the 1980s, related to the increase in irrigated rice production in Africa. Increased production led to host-plants being available during the dry season, but more importantly, hardier, long-duration rain-fed rice varieties were replaced by softer, short-duration, irrigated varieties. In paddy fields, both the swarms of stalk-eyed flies and the apparent damage they cause (so-called "dead heart") are highly visible and lead to complaints by farmers.

The larvae of *D. longicornis* are obligate borers in *Oryza* species, especially attacking the cultivated varieties, but also African wild rice, *O. barthii* A.Chev (Descamps 1957: 122). Females begin oviposition as soon as the rice seedlings are a few centimetres high. In transplanted fields, the highest egg densities are reached after four weeks (Feijen & Schulten 1981), while no further eggs are laid after eight weeks. Controversy exists about the number of stems attacked by a single larva. Descamps stated that a single larva destroys an average of three stems, but this was based on circumstantial evidence. Brenière (1969) and Jordan (1966: 27) quoting Descamps increased the number of stems destroyed to 6, up to 10. Feijen (1979) and Feijen *et al*. (1979: 279), however, reported that larvae can only kill small rice seedlings. In stems longer than *ca* 10 cm, only the terminal leaf dies-off (the "dead heart"), but the stem will produce new terminal leaves, although these can also die due to the feeding action of the same larva. In this way, one larva can produce up to four successive dead hearts on the same stem, although usually only one or two are produced. The larva remains in the same stem until just prior to pupariation in a leaf axil, except when it attacks small seedlings.

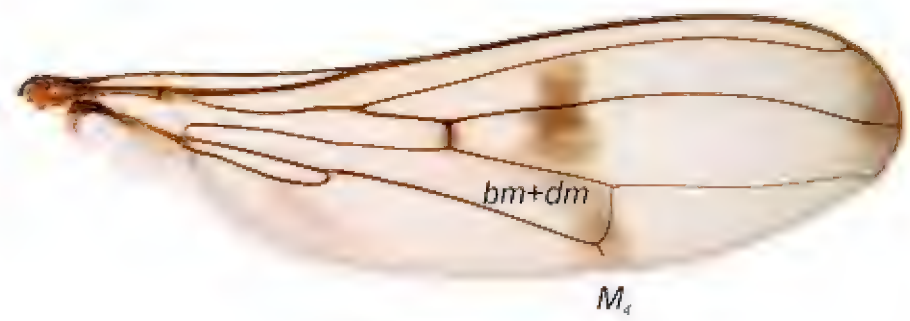
Accurate yield-loss assessments are scarce. Although damage can, initially, look severe, rice plants can often compensate. In

Ghana, Abu (1972) investigated experimentally the effects on tillering after attacks by *D. longicornis*. In Malawi, the results of experiments simulating injuries caused by *D. longicornis* larvae indicated that they may have both negative or positive effects on rice (Feijen 1979). Under normal conditions, the effect on yield was considered positive or neutral, while the effect only becomes negative if poor growing conditions are combined with a late, heavy attack. Nevertheless, this paper was several times quoted with the rather selective remark that yield-losses in Malawi amounted to 23% (e.g., Walker 1987). Feijen (1989: 59), considered that claims of yield-losses up to 97% could not be taken seriously. Vercambre (1982) reported that the effect of *D. longicornis* larvae on the yield could be positive (e.g., 28% more) or negative (e.g., 15% less), depending on level of attack and variety. Chiasson & Hill (1993) reported that in a single cropping system in Guinea neither *D. apicalis* nor *D. longicornis* were serious pests of rice.

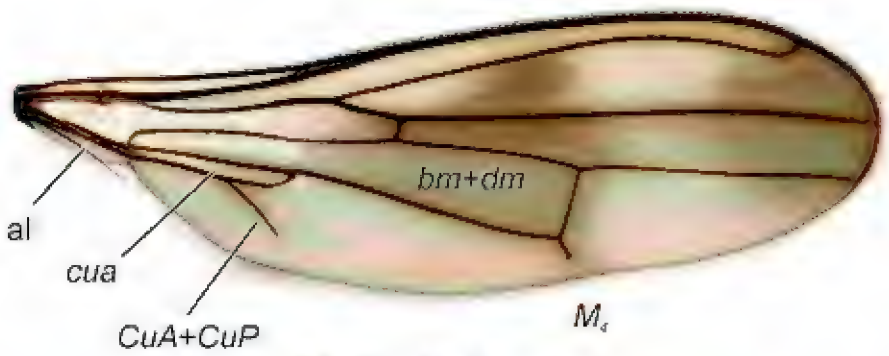
The economic importance of *D. longicornis* is much less than has often been claimed. Compensatory tillering is a key aspect, although this depends on the rice variety and growing conditions. Nevertheless, fields of young rice with almost



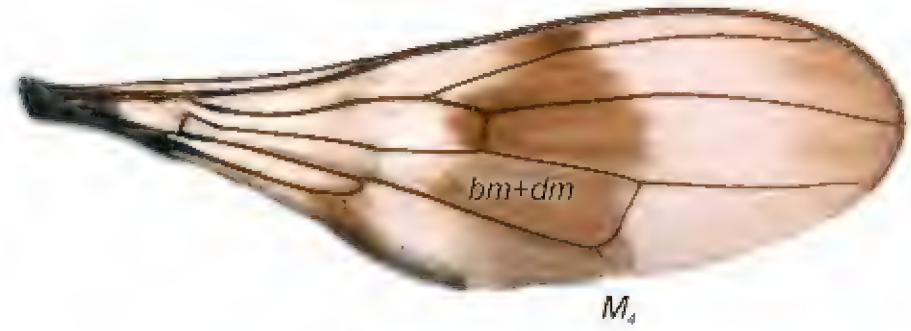
16 *Centrioncus* ♀



17 *Chaetodiopsis* ♀

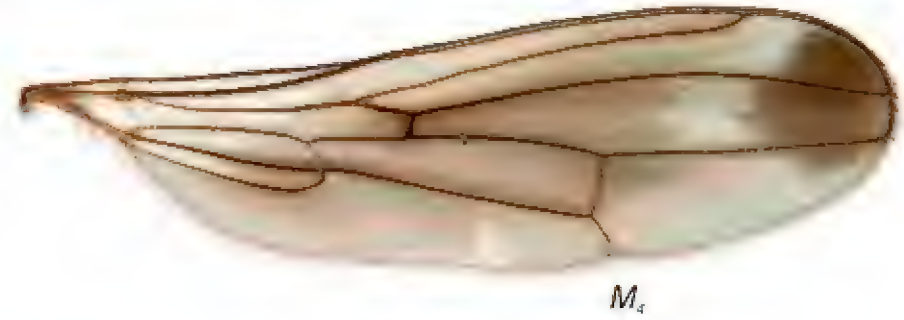


18 *Cladodiopsis* ♀



19 *Cobiopsis* ♂

20 *Diopsina* ♂



21 *Diopsis* ♀

22 *Diopsis* ♀

Figs 64.16–22. Wings of Diopsidae (dorsal views): (16) *Centrioncus jacobae* Feijen ♀; (17) *Chaetodiopsis meigenii* (Westwood) ♀; (18) *Cladodiopsis leptophylla* Séguy ♀; (19) *Cobiopsis latifascia* (Brunetti) ♂; (20) *Diopsina kwaipai* Feijen ♂; (21) *Diopsis atricapilla* Guérin-Méneville ♀; (22) *D. longicornis* Macquart ♀.

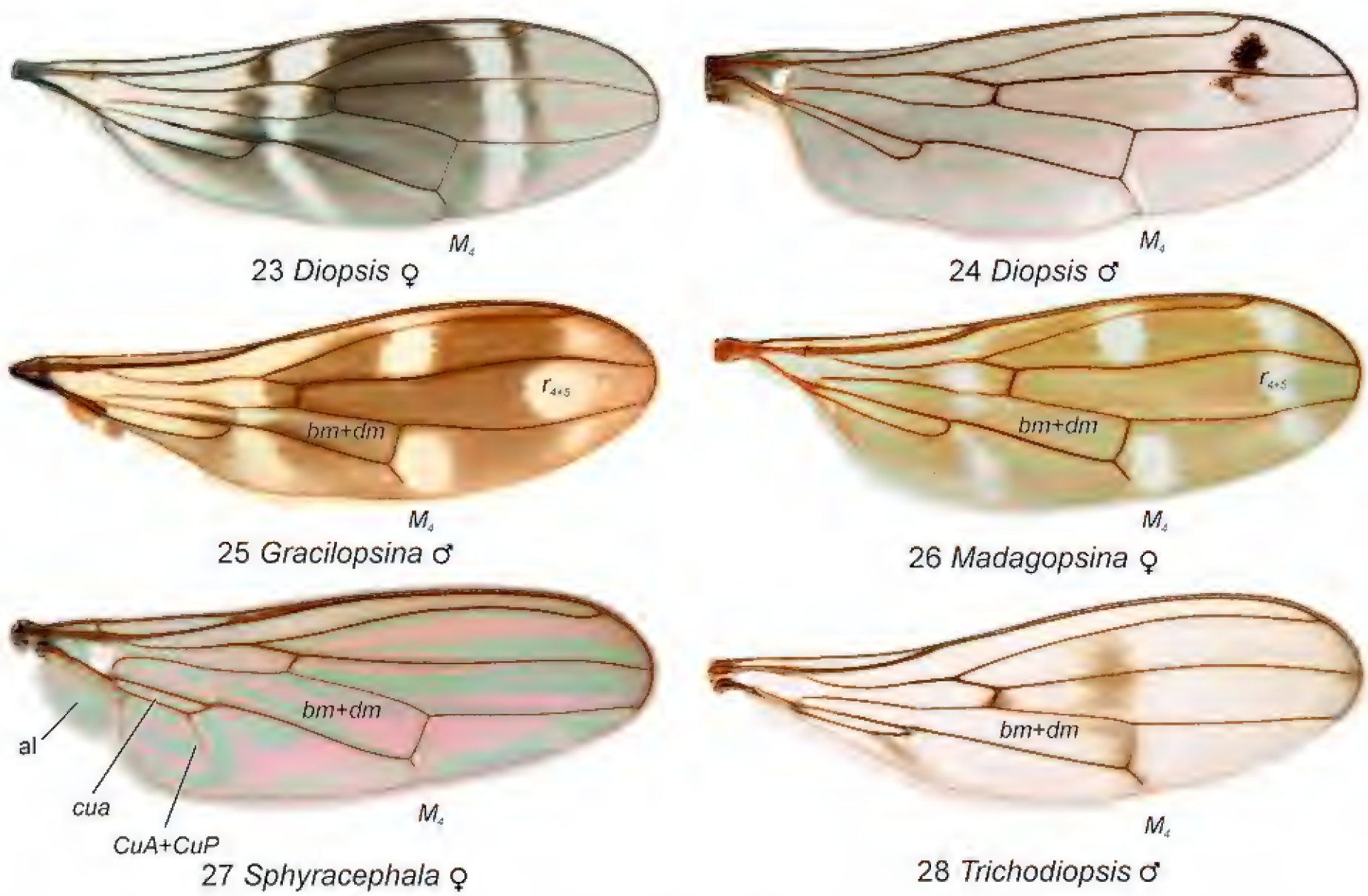
Abbreviations: al – alula; *bm+dm* – basal medial cell + discal medial cell; *br* – basal radial cell; *C* – costal vein; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *dm–m* – discal medial crossvein; M_1 – first branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein.

all tillers attacked do occur. In such cases, a good extension system is required to explain the issue to farmers. Chemical control is normally not necessary, except in some instances in nurseries. Spraying is especially counterproductive, as it interferes with the rate of egg parasitism. In Zanzibar, the rice crop was until 1983 regularly sprayed against *D. longicornis*, so egg parasitism was well below 10%. Following the termination of spraying egg parasitism climbed back to its normal end of season levels of *ca* 90%.

Diopsis longicornis was reared from Maize in Zanzibar on one occasion and other *Diopsis* species have been reported from graminaceous crops in Africa, but these can only be considered as marginal pests and often occur as secondary borers. The West African *D. apicalis* is the most frequently mentioned species (Jordan 1966: 28; Morgan & Abu 1973; Scheibelreiter 1974). In East and Southern Africa, the very common *D. mayae* and several other, but rare, species of the *D. apicalis* species-group are secondary borers in Maize, Sorghum, *Sorghum bicolor* (L.) Moench, and rice (Feijen & Feijen 2017). Species, such as *Chaetodiopsis meigenii* (Westwood, 1837), *Diasemopsis fasciata* (Gray, 1832) and *D. obstans* (Walker, 1861), have been reported from rotting rice, millet and sugarcane waste (Bruggen 1961: 416; Descamps 1957: 120). Bijlmakers (1990: 25) recorded a *Diopsis* species as a minor pest of Sorghum in Ethiopia. There are only infrequent reports of diopsids attacking crops in Asia. Tan (1965) was able to rear a species of the *Diopsis indica* Westwood, 1835 species-group on young Maize. In Bhutan, however, two species of the *D. indica* species-group acted as secondary stem-borers of Maize, following primary lepidopterous borers.

Classification

The concept of the family Diopsidae dates back to Billberg (1820: 115), who created the natio Diopsides, placing it between the Muscides and the Conopides. Feijen (1989: 3) presented an historical overview of the placement of the Diopsidae within Diptera. Although views on its affinities were diverse, Diopsidae were up until 1920 often placed as the subfamily Diopsinae of the Muscidae. Frey (1921) and Hendel (1922) stressed a relationship with non-Afrotropical Megamerinidae and the Sepsidae. Shillito (1950) transferred the stalkless genus *Centrioncus* from Sepsidae to Diopsidae. Bruggen (1961: 415) considered the systematic position of the Diopsidae obscure, but assumed a close relationship with Psilidae and Sepsidae. Hennig (1958) grouped the Diopsidae, together with



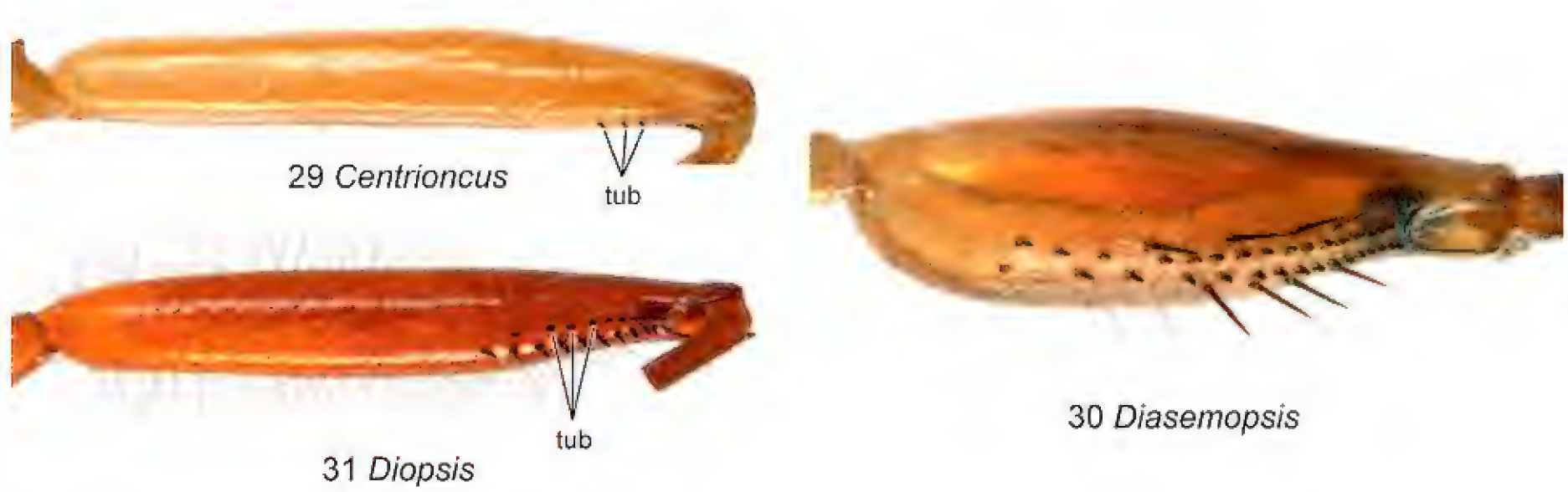
Figs 64.23–28. Wings of Diopsidae (dorsal views): (23) *Diopsis nigra* Illiger ♀; (24) *D. somaliensis* Johnson ♂; (25) *Gracilopsina vadoni* (Vanschuytbroeck) ♂; (26) *Madagopsina parvapollina* Feijen, Feijen & Feijen ♀; (27) *Sphyracephala munroi* Curran ♀; (28) *Trichodiopsis horni* (Curran) ♂. Figs 25, 26 (Feijen *et al*. 2018, figs 11, 7, respectively).

Abbreviations: al – alula; *bm+dm* – basal medial cell + discal medial cell; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; M_4 – fourth branch of media; r_{4+5} – fourth + fifth radial cells.

the Megamerinidae, Nothybidae, Psilidae, Tanypezidae and Strongylophthalmyiidae (all except Psilidae non-Afrotropical), in the superfamily Nothyboidea. Within this superfamily he recognised a closer relationship between Diopsidae, Megamerinidae and Nothybidae. Hennig agreed with the inclusion of *Centrioncus* in the Diopsidae. Hennig (1973: 53) added the non-Afrotropical Syringogastridae to the Nothyboidea. Prado (1969) had erected the Neotropical Syringogastridae for *Syringogaster* Cresson, earlier included in the Megamerinidae. Griffiths (1972: 113) revised Hennig's tentative superfamily Nothyboidea and only included Nothybidae, Periscelididae, Psilidae and non-Afrotropical Teratomyzidae. The Megamerinidae were placed in the prefamily Sciomyzoinea and the Tanypezidae (including Strongylophthalmyiidae) in the prefamily Tanypezoinea. The Diopsidae and Syringogastridae were placed as sister-groups in the prefamily Diopsioinea. Feijen (1983) assumed only the subfamily Centrioncinae of the Diopsidae to have a sister-group relationship to the Syringogastridae and elevated this subfamily to family-level.

McAlpine (1989: 1432), followed Hennig's (1958, 1973: 53) grouping Nothyboidea (also referred to as Tanypezoidea), but renamed this the superfamily Diopsoidea. Within this superfamily McAlpine distinguished two sister-groups, one consisting of Strongylophthalmyiidae and Tanypezidae and the other of Diopsidae, Megamerinidae, Nothybidae, Psilidae, non-Afrotropical Somatiidae and Syringogastridae, indicating a closer relationship again between the families Diopsidae, Megamerinidae, Nothybidae and Syringogastridae. The Diopsidae were considered the sister-group to the Megamerinidae + Syringogastridae. McAlpine (1997*a*), included in the Diopsoidea the Diopsioinea (Diopsidae + Syringogastridae) and the "ungrouped" non-Afrotropical Gobryidae, Nothybidae and Psilidae. McAlpine (1997*b*), placed the Megamerinidae in the Nerioidea, while leaving Somatiidae, Strongylophthalmyiidae and Tanypezidae unplaced. Meier & Hilger (2000) included Centrioncidae again within the Diopsidae and indicated the Syringogastridae as the likely sister-group to the Diopsidae.

Following publication of a set of phylogenetic studies at molecular level on relations between families within the Acalyptratae, the paraphyly of what Hennig (1958: 506) already called the "sogenannten Acalyptratae" remains disputed, while delimitations of various superfamilies and relationships between a number of families remain uncertain (Caravas & Friedrich 2012; Woodley *et al*. 2009: 86). The relatively low level of taxon sampling within the Acalyptratae is indicated as the main reason for the lack of a firm theory on the phylogeny of the Acalyptratae and its place within the Schizophora (Gibson *et al*. 2010; Woodley *et al*. 2009: 86). As far as the placement of the Diopsidae is concerned, various theories have been proposed. Han *et al*. (2002), proposed a sister-group relationship between Conopidae and Diopsidae, a view curiously close to Billberg's (1820: 115) ideas. Han & Ro (2005) considered the Conopidae and Diopsidae as possibly the most early branching groups among the schizophoran families included in their study. Marshall *et al*. (2009) were confident that the Diopsidae (including Centrioncinae), were the sister-group of Syringogastridae and proposed the Megamerinidae as the sister-group to Syringogastridae + Diopsidae. Lambkin *et al*. (2012), in a study based on morphological evidence, stated that it was premature to discuss hypotheses on Acalyptratae phylogeny in greater detail. They indicated, however, a "near-basal" position in the Schizophora of the Diopsidae and Psilidae and the Conopidae as sister-group to all remaining Schizophora in their selection of families. Wiegmann *et al*. (2011) provided a phylogenomic estimate of fly relationships, based on molecules from 149 of 157 families. They considered relationships among schizophorans as poorly supported, with the available data and their robust resolution remains a major challenge for animal phylogenetics. In the Schizophora, they distinguished a paraphyletic grade of acalyptrate flies and a monophyletic Calyptratae. The Diopsidae were placed as sister-group to the Marginidae + Nannodastiidae + Canacidae, while the Syringogastridae were placed remarkably distant and as sister-group of the Psilidae. In a review of the Strongylophthalmyiidae and Tanypezidae, based on a morphological character matrix, Lonsdale (2013) found in a limited outgroup selection a *Centrioncus* species and a *Sphyracephala* species in a clade with a *Nothybus* Rondani species (Nothybidae) and a *Formicosepsis* de Meijere species (non-Afrotropical Cypselosomatidae) and not as sister-groups. In a broader study, Lonsdale (2020) reviewed the superfamily Diopsoidea. Based on a morphological



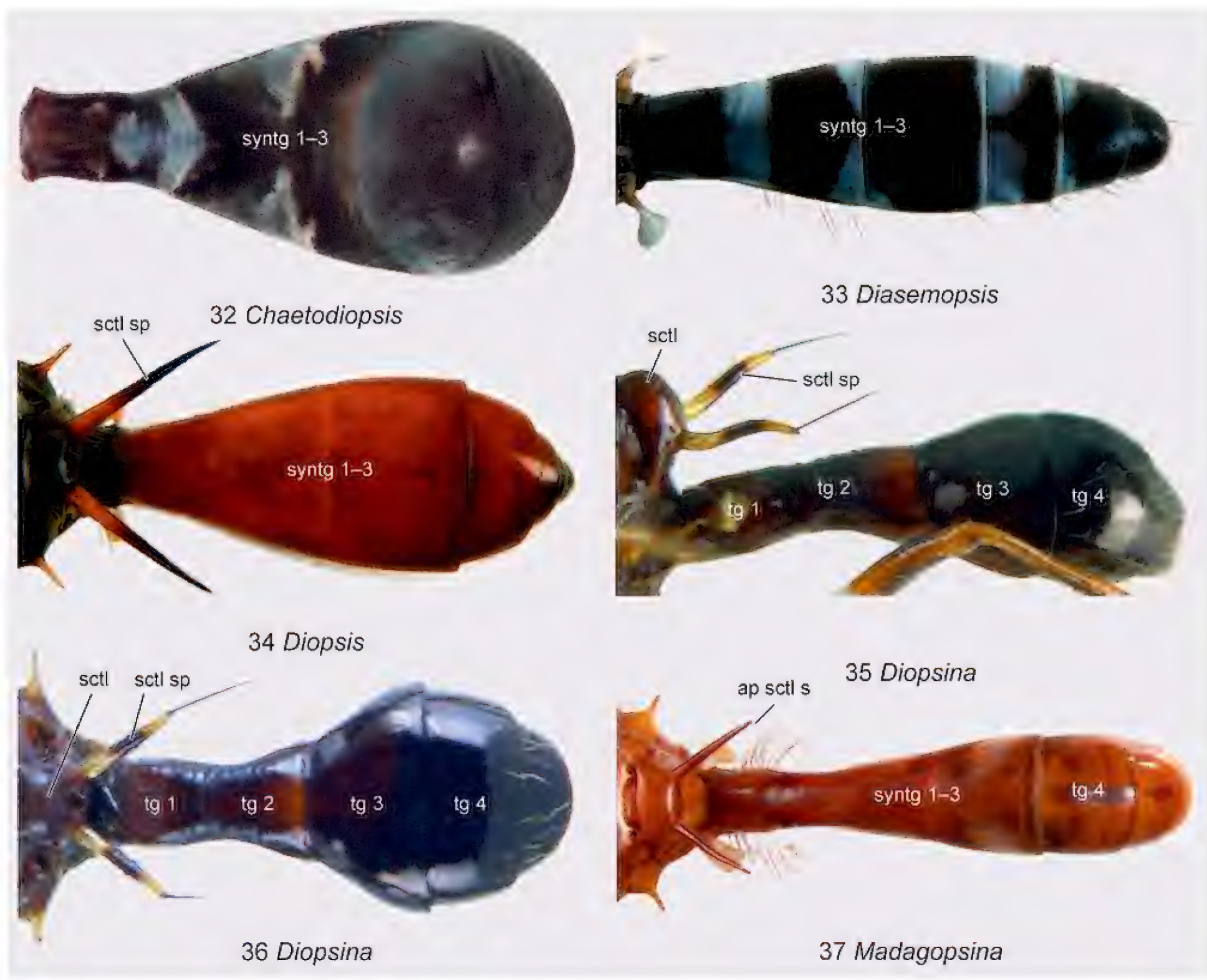
Figs 64.29–31. Femora of Diopsidae (ventrolateral views): (29) hind femur of *Centrioncus decoronotus* Feijen ♂; (30) fore femur of *Diasemopsis silvatica* Eggers ♀; (31) same, *Diopsis longicornis* Macquart ♂.

Abbreviation: tub – tubercles.

phylogenetic analysis, he concluded that the Diopsoidea contains a core group of families that are strongly supported as monophyletic: Diopsidae, Megamerinidae and Syringogastridae. In a most parsimonious tree, Diopsidae were placed as sister-group to the Syringogastridae and these two families together as sister-group of the Megamerinidae.

Hennig (1965: 62) divided the family into the Centrioncinae and Diopsinae. The latter subfamily he subdivided into the "Stammgruppe" Prosphyracephala and the tribes Sphyracephalini and Diopsini. Shillito (1971) recognised three subfamilies: Centrioncinae, Diopsinae and Sphyracephalinae. Steyskal (1972) followed Hennig's system, although rearranging the genera. Feijen (1989: 11) distinguished Centrioncidae and Diopsidae; the latter divided into Sphyracephalinae and Diopsinae. Meier & Baker (2002) discussed the phylogenetic relationships and retained the system with two subfamilies and two tribes. In the following paragraphs the system of three subfamilies is followed and a brief overview is given of each subfamily.

Centrioncinae stand apart in the Diopsidae as they lack eye stalks. They only occur in sub-Saharan Africa and can be recognised by their slender build, the tripartite pubescent antennal arista, two pairs of head setae, three pairs of scutal setae, the apical scutellar setae as long as the pair of scutellar spines, the presence of an alula, wing veins *CuA+CuP* and M_4 reaching the wing margin, the incrassate fore femur with rows of tubercles and spinous setae, the hind femur with some tiny tubercles and the abdominal syntergite only consisting of tergites 1–2. Speiser (1910: 190) placed *Centrioncus prodiopsis* Speiser, 1910 in the Sepsidae, indicating the resemblance



Figs 64.32–37. Abdomens of Diopsidae: (32) *Chaetodiopsis meigenii* (Westwood), dorsal view ♀; (33) same, *Diasemopsis varians* Eggers ♂; (34) same, *Diopsis mayae* Feijen & Feijen ♀; (35) *Diopsina fluegeli* Feijen & Feijen, lateral view ♂; (36) same, dorsal view; (37) same, *Madagopsina freidbergi* Feijen, Feijen & Feijen ♂. Figs 35, 36 (Feijen & Feijen 2013, figs 21, 22).

Abbreviations: ap sctl s – apical scutellar seta; sctl – scutellum; sctl sp – scutellar spine; syntg – syntergite; tg – tergite.

to a stalkless "*Diopsis*". Feijen (1983) elevated the subfamily to family status, a view that was not later followed. He also added the second genus *Teloglabrus*, provided an identification key and suggested the vernacular name "Afromontane forest flies".

Sphyracephalinae includes two extant genera and one extinct genus. They have a wide distribution and occur in the Holarctic Realm and in the Afrotropical, Australasian and Oriental Regions. These early branching stalk-eyed flies are characterised by a tripartite glabrous antennal arista, 1–2 pairs of scutal setae, the apical scutellar setae much longer than the scutellar spines, presence of an alula, wing vein *CuA+CuP* extending past cell *cua*, vein M_4 extending beyond cell *bm+dm* or not (but not reaching margin) and the abdominal syntergite only consisting of tergites 1–2.

Diopsinae includes 13 genera and occurs in the Afrotropical and Oriental Regions. They also occur at the borders of the Palaearctic Region (Feijen *et al*. 2017). These stalk-eyed flies are characterised by the bipartite, glabrous (or virtually glabrous) antennal arista, the apical scutellar seta are absent or present (if present, then usually shorter than the scutellar spines), the absence of an alula (highly reduced alulas occur in some species of the *Diasemopsis* genus-group), wing vein *CuA+CuP* absent, vein M_4 extending beyond cell *bm+dm* (reaching margin or not) and abdominal syntergite including tergites 1–3. Based on nuclear markers, Feijen *et al*. (2018) distinguished three clades in the Diopsinae: the early branching *Diasemopsis* genus-group, the *Teleopsis* genus-group and the genus *Diopsis*. The *Diasemopsis* genus-group (Feijen 1989: 60), consists of *Chaetodiopsis*, *Cobiopsis*, *Diasemopsis* and *Trichodiopsis*. The genera *Chaetodiopsis*, *Diasemopsis* and *Trichodiopsis* were placed into synonymy by Meier & Baker (2002) and Shillito (1971). Although concurring with the evidence that *Chaetodiopsis* and *Trichodiopsis* are embedded within the present concept of *Diasemopsis*, it is here preferred to maintain these genera, until a revision of *Diasemopsis sensu lato* has resolved the groups within the genus and has considered the options to split it up into a number of genera. The *Diasemopsis* genus-group is characterised by the dual presence of rows of tubercles and spinous setae on the fore femur (Fig. 30) and by the presence of only two spermathecae. Feijen & Feijen (2013) discussed the possible monophyly of Diopsidae genera with irrorated wings. Feijen *et al*. (2018) showed that, based on nuclear markers, the genera with irrorated wings indeed form a monophyletic group and named it the *Teleopsis* genus-group. If mitochondrial markers are included, however, the genus *Diopsis* also warrants a place within this group. In the Afrotropical Region the group is represented by *Diopsina*, *Gracilopsina* and *Madagopsina*, while in the Oriental Region five additional genera occur, namely: *Cyrtodiopsis*, *Eosiopsis* Feijen, *Eurydiopsis* Frey, *Megalabops* and *Teleopsis*. The group is easily characterised by the irrorated wings (Figs 20, 25, 26). The third clade is formed by *Diopsis*, a large genus that at a later stage will have to be split. It is easily recognised by vein M_4 reaching the wing margin and the absence of an apical seta on the scutellar spines.

Identification

Keys to world genera were provided by Feijen (1989: 64), Séguy (1955), Shillito (1971) and Steyskal (1972). Steyskal also included a catalogue to the entire family, while Cogan & Shillito (1980: 583) and Descamps (1957: 13) provided catalogues for Afrotropical species. These identification keys are now outdated and should only be consulted in combination with more recent phylogenetic works (Kotrba *et al*. 2010; Meier & Baker 2002) and comments (Feijen 2011; Feijen & Feijen 2013). Meier & Hilger (2000) provided an identification key to a large number of genera based on egg morphology. Diopsidae are best micro-pinned in the field for later double-mounting (see Chapter 2).

Key to genera of Afrotropical Diopsidae

1. Head rounded, with eyes and antennae not on stalks (e.g., Figs 2, 3); antennal arista 3-articled, pubescent; wing vein *CuA+CuP* reaching wing margin (e.g., Fig. 16); hind femur with some tiny tubercles (e.g., Fig. 29); male terminalia with surstylus 3-lobed, with tubercles (e.g., Fig. 47) (CENTRIONCINAE) 2

– Head not rounded, with eyes and antennae at end of lateral stalks (e.g., Figs 1, 4–8, 11, 12); antennal arista 2- or 3-articled, bare or virtually so; wing vein *CuA+CuP* absent (e.g., Fig. 17), or if present, not reaching wing margin (e.g., Fig. 18); hind femur without tubercles; male terminalia with surstylus relatively simple (e.g., Figs 48–50), with at most one apophysis, without tubercles 3

2. Palpus dark (Fig. 2); wing with central macula (Fig. 16); female abdominal sternite 7 (Fig. 44) with single anterior rectangular sclerite and single, strongly curved or rectangular posterior sclerite; male terminalia with epandrium broad, rounded, with width/length ratio: 1.4–1.5; ejaculatory apodeme and sac very large (9.2–16.3% of body length); ejaculatory duct near sac perpendicular to apodeme; outer surstylus pruinescent (Figs 46, 47) (Angola, East and West Africa, north of Zambesi River) . . . . . *Centrioncus* Speiser

– Palpus usually yellow; wing usually without central wing macula; female abdominal sternite 7 (Fig. 45) with two sclerites anteriorly narrowly connected on meson and two small posterior sclerites present or absent; male terminalia with epandrium rather narrow, bell-shaped, with width/length ratio: 1.0–1.1 (1.2–1.3 in some species); ejaculatory apodeme and sac normal-sized (5.6–8.4% of body length); ejaculatory duct near sac more or less in line with apodeme; outer surstylus bare (south of Zambesi River) . . . . . *Teloglabrus* Feijen

3. Antennal arista 3-articled; wing with alula; vein *CuA+CuP* extending beyond cell *cua* (e.g., Figs 18, 27); scutellar spine with apical seta longer than spine (e.g., Fig. 4); abdominal syntergite comprising tergites 1–2 (SPHYRACEPHALINAE) 4

– Antennal arista 2-articled; wing without alula; vein *CuA+CuP* absent (e.g., Figs 20–21); scutellar spine with apical seta usually shorter than spine or absent; abdominal syntergite comprising at least tergites 1–3 (DIOPSINAE) 5

4. Head with eye stalks slender (0.25–0.40 × widest sagittal eye diameter, Fig. 5); scutum with 1 pair of strong intra-alar setae (in one species also weak presutural setae); scutellar spine with apical seta < 2 × spine length; wing with alula reduced; vein *CuA+CuP* branching-off well before apex of cell *cua* (Fig. 18) (confined to Comoros and Madagascar) . . . . . *Cladodiopsis* Séguy

– Head with eye stalks stout (0.65–0.80 × widest sagittal eye diameter, Fig. 4); scutum with 2 pairs of strong setae (intra-alar seta and presutural seta); scutellar spine with apical seta > 3 × spine length; wing with alula well-developed; vein *CuA+CuP* branching-off near apex of cell *cua* (Fig. 27) (continental Afrotropics, Madagascar, Southern Arabian Peninsula) . . . . . *Sphyracephala* Say

5. Fore femur with 2 rows of spinous setae surrounding 2 rows of tubercles (e.g., Fig. 30); scutellar spine with apical seta; abdomen usually dark, with intricate pattern of silvery grey pruinescence (e.g., Figs 32, 33); female with 2 (1 + 1) spermathecae (*Diasemopsis* genus-group) 6

– Fore femur with 2 rows of tubercles, but without spinous setae (e.g., Fig. 31); scutellar spine with apical seta present or absent; abdomen yellowish, reddish or dark, with (if present) only reduced and obscure pruinescence (e.g., Figs 34–37); female with 3 (2 + 1) spermathecae 9

6. Thorax with intra-alar spine (Figs 8, 9); with strong, straight, laterally directed pleurotergal spines (Figs 8, 9); scutum without setae (Figs 8, 9); fore and mid femora with 2 and 3 apical spurs respectively; abdomen with syntergite consisting of tergites 1–4 . . . . . *Cobiopsis* Feijen

– Thorax without intra-alar spine (e.g., Fig. 10); pleurotergal spines mostly posterolaterally directed; scutum with 1 or 2 pairs of setae (e.g., Fig. 10); fore and mid femora without apical spurs; abdomen with syntergite consisting of tergites 1–3 only (e.g., Figs 32, 33) 7

7. Head with outer vertical seta stout; inner vertical seta large, inserted on distinct tubercle (Figs 11, 12); wing membrane largely without microtrichia (Fig. 28); thorax without presutural seta; intra-alar seta large, strong and erect, inserted on distinct tubercle; scutellum with spines strongly curved upward (Fig. 11); abdominal segment 2 with subtle basal constriction . . . . . *Trichodiopsis* Séguy

– Head with outer vertical seta small to moderately sized; inner vertical seta tiny to large, not inserted on distinct tubercle; if outer vertical seta stout and inner vertical seta on tubercle, then wing membrane with only minimal (mainly basal) sections without microtrichia (e.g., Fig. 17); thorax with presutural seta present or absent (e.g., Fig. 10); intra-alar seta simple, not erect, not inserted on distinct tubercle; scutellum with spines usually more or less straight, not strongly curved upward (e.g., Fig. 10); abdominal segment 2 without basal constriction (e.g., Figs 32, 33) 8

8. Thorax without presutural seta; wing with narrow central band and small apical macula (Fig. 17); abdomen distally broad and rounded (Fig. 32); male terminalia with distinct suture between surstyli and epandrium; female spermathecae bulb-shaped, with abrupt transition between spermatheca and duct . . . . . *Chaetodiopsis* Séguy

– Thorax with presutural seta present or absent; wing various, but without combination of narrow central band and small apical macula; abdomen usually slender, pointed apically (Fig. 33); male terminalia without suture between surstyli and epandrium; female spermathecae elongate, with gradual transition between spermatheca and duct . . . . . *Diasemopsis* Rondani

9. Head with inner vertical seta tiny or spinous; wing membrane either hyaline without maculae, or virtually uniformly greyish, or with dark central, preapical or apical maculae (Figs 1, 21–24); vein M_4 reaching wing margin (Figs 21–24); scutellar spine without apical seta; abdomen with syntergite 1–3 appearing as single sclerite (Fig. 34) . . . . . *Diopsis* L.

– Head with inner vertical seta distinct, not spinous; wing membrane brownish to dark, irrorated, with 3 bands of pale maculae (e.g., Figs 20, 25, 26); vein M_4 not reaching wing margin (e.g., Figs 20, 25, 26); scutellar spine with apical seta; abdomen with syntergite 1–3 with distinct seam between tergites 2 and 3 (e.g., Figs 35–37) (*Teleopsis* genus-group) 10

10. Small- to medium-sized flies (body length: 3.0–5.8 mm); scutellum swollen, deeper than long; scutellar spines with dark central section, pale base and tip (Figs 35, 36); with strong apical scutellar seta, 0.49–1.20 × length of spine (Figs 35, 36); abdomen strongly clavate, tergites 1 and 2 small, tergites 3 and 4 largest and widest (Fig. 36); sexual monomorphism with respect to eye span (continental Afrotropics only) . . . . . *Diopsina* Curran

– Medium- to large-sized flies (body length: 5.4–10.2 mm); scutellum quite flat, not deeper than long; scutellar spines concolourous; with weak apical scutellar seta, < 0.45 × length of spine, often absent (e.g., Fig. 37); abdomen very slender to moderately club-shaped, tergite 1 small, tergite 2 largest, tergites 3 and 4 widest (e.g., Fig. 37); sexual dimorphism with respect to eye span (confined to Madagascar) 11

11. Body dark brown to blackish; scutum glossy (Fig. 7); head with inner vertical seta > 2.9 × eye stalk diameter; prosternum fused to proepisternum forming precoxal bridge (Fig. 15); wing with pale preapical wing band in cell r_{4+5} strongly convex proximally (Fig. 25); fore coxa glossy (Fig. 15); abdominal tergites 2 and 3 with large mesal triangular pruinescent maculae; anterior section of sternite 2 laterally linked to main sternite 2 (Fig. 43); ratio of length of sternites 1 + 2 + 3/width posterior sternite 2 6.0–10.6; male terminalia with surstylus without apophysis, fused to epandrium . . . . . *Gracilopsina* Feijen, Feijen & Feijen

– Body glossy yellowish brown (Fig. 6); scutum thinly pruinescent; head with inner vertical seta 0.8–2.3 × eye stalk diameter; basiliform prosternum (Fig. 14); wing with pale preapical wing band in cell r_{4+5} barely convex proximally (Fig. 26); fore coxa pruinescent anteriorly and/or on inner side (Fig. 14); abdominal tergites 2 and 3 uniformly glossy, or thinly pruinescent, in some species with 2 posterolateral pruinescent maculae on tergite 3 (Fig. 37); anterior line-like section (intersternite 1–2) of sternite 2 not linked to main sternite 2 (Fig. 42); ratio of length of sternites 1 + 2 + 3/width posterior sternite 2 2.8–4.8; male terminalia with surstylus with large apophysis, articulated . . . . . *Madagopsina* Feijen, Feijen & Feijen

Synopsis of the fauna

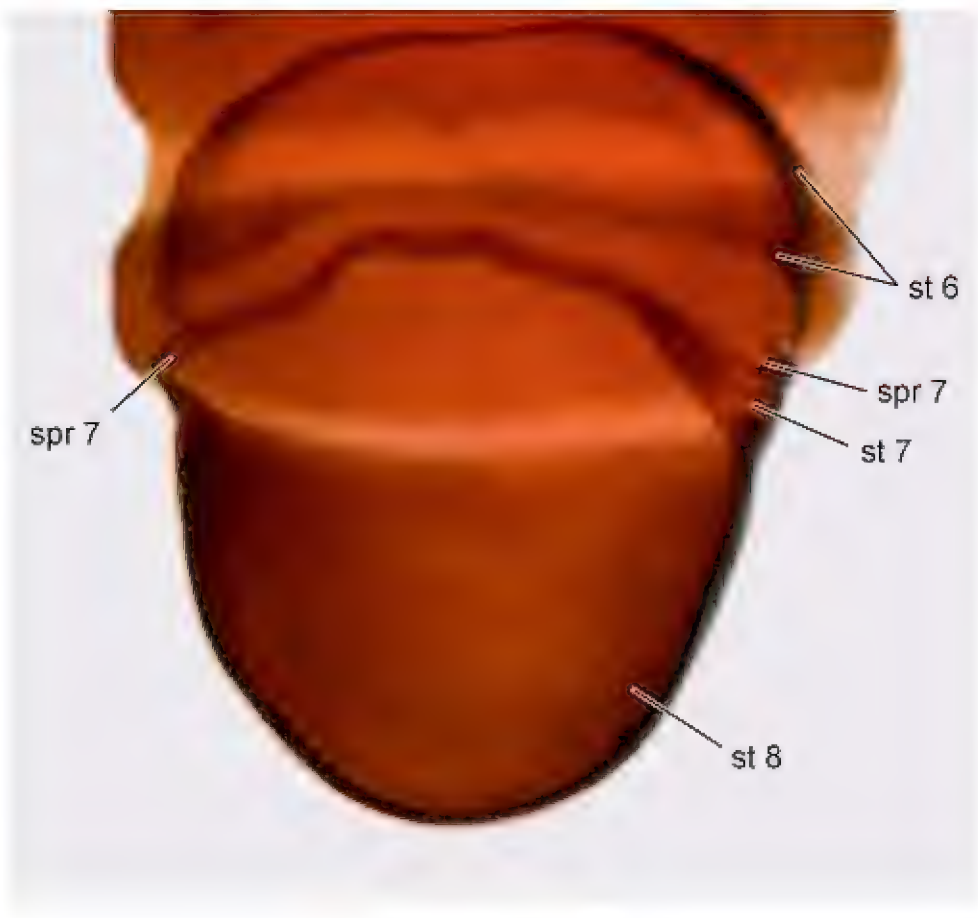
There are 17 genera of Diopsidae currently recognised globally (Feijen 1989: 61, 2011; Feijen & Feijen 2013; Feijen *et al.* 2018), of which 12 occur in the Afrotropical Region. About 239 species are recognised in the world fauna. In addition, three fossil species are placed in *Prosphyracephala* Hennig. In the Afrotropical Region, 157 species occur, but there are numerous undescribed species, especially in *Diasemopsis* and *Diopsis*. Various Afrotropical diopsids originally assigned to the genera *Cyrtodiopsis*, *Eurydiopsis* and *Teleopsis* (now all considered as purely Oriental), were later re-assigned to Afrotropical genera. Only the genera *Diopsis* and *Sphyracephala* occur in both these regions. Diopsidae are not known from the Atlantic Ocean Islands, while for the Indian Ocean Islands they are only known to occur in Comoros and Madagascar. Six Diopsidae species occur in the Southern Arabian Peninsula (Feijen *et al.* 2017).

***Centrioncus* Speiser** (Centrioncinae)**.** An endemic genus (Fig. 2) of seven described species, distributed in East and West Africa to the north of the Zambezi River. An undescribed species is known from Angola and few additional species should still be expected. Species appear to have very limited, allopatric distribution ranges, with the exception of *C. aberrans* Feijen, 1983, which occurs in Kenya, Rwanda and Uganda. The genus remained monotypical, until Feijen (1983) described five additional species and De Meyer (2004) added the seventh. This stalkless genus (Fig. 2) can be distinguished from the second stalkless genus, *Teloglabrus* (Fig. 3), by the dark palpus, the presence of a vague central wing macula (Fig. 16), the absence of distal fasciae on the hind femur, the male terminalia with a broad and rounded epandrium with a width/length ratio of 1.4–1.5, the microtrichose outer and median arms of the surstylus (Fig. 47), the very large ejaculatory apodeme and female sternite 7 (Fig. 44) split into a broad, rectangular anterior plate and a curved or rectangular posterior plate (the latter misinterpreted as sternite 8 by De Meyer 2004 and Feijen 1983). All species occur in Afromontane forests, usually well above 1000 m elevation, but the West African species occurs at *ca* 200 m. Some information on ecology was provided by Feijen (1983). Flies occur in the darker, more humid parts of the forest on small shrubs and reproduction begins towards the end of the dry season. Biology and immature stages remain unknown. Feijen (1983) provided an identification key to six Afrotropical species.

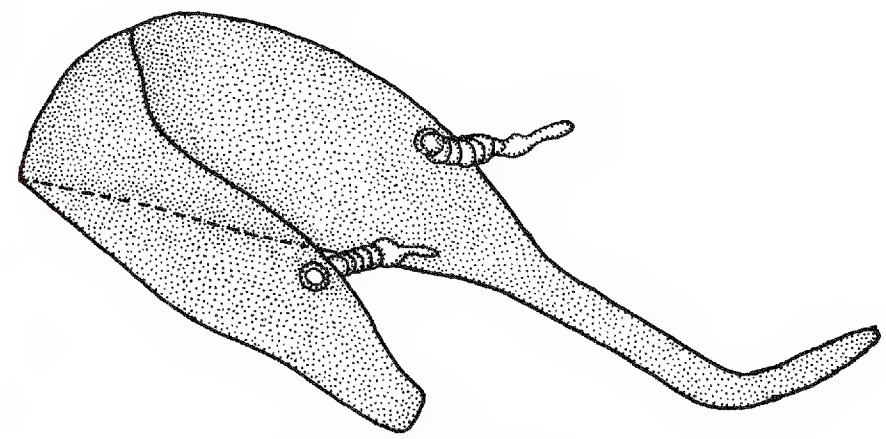
***Chaetodiopsis* Séguy** (Diopsinae)**.** An endemic genus of two described species: *C. comoroensis* (Carr & Földvári, 2006), described from Comoros (Carr *et al.* 2006); and *C. meigenii*, the commonest sub-Saharan diopsid, widely distributed in the continental Afrotropics and even extending into Oman in the Southern Arabian Peninsula (Feijen *et al.* 2017). The genus is one of the four genera comprising the *Diasemopsis* genus-group. Séguy's (1955) basis for erecting the genus of three species was weak and Feijen (1989: 63) revised it to include only the type species. Carr *et al.* (2006), Meier & Baker (2002) and Shillito (1971), included *Chaetodiopsis* as a junior synonym of *Diasemopsis*. The genus is maintained here, until such time as the entire *Diasemopsis* genus-group has been resolved. Distinguishing characters are the male terminalia with an articulated surstylus (fused to the epandrium in *Diasemopsis*), the wing pattern (Fig. 17), the strongly clavate and apically rounded abdomen (Fig. 32) and the bulb-shaped spermathecae, with an abrupt transition between spermatheca and duct. An identical wing pattern is apparent in *Trichodiopsis* (Fig. 28), but the wing cell shapes and microtrichia patterns differ. *Chaetodiopsis meigenii* is often found on rotting fruit near human habitation, but also in (secondary) rainforest. Thousands of specimens were once observed in a fruit market in Maputo, Mozambique (H. Feijen, pers. obs.). It is one of the very few diopsids that is attracted to artificial lights and regularly enters houses. The egg was described by Meier & Hilger (2000), while all immature stages were described by Descamps (1957: 40). An identification key to the two species was provided by Carr *et al.* (2006).

***Cladodiopsis* Séguy** (Sphyracephalinae)**.** An endemic genus (Fig. 5) of three described species: *C. leptophylla* Séguy,

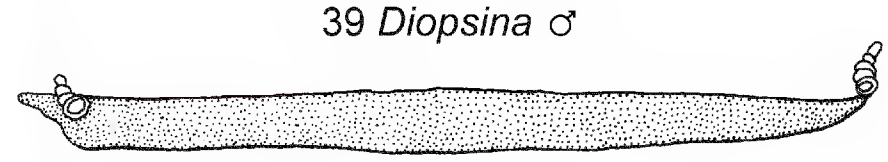
1949; *C. seyrigi* Séguy, 1949 and *C. sicardi* Séguy, 1949, all confined to Madagascar (Séguy 1949). Two additional Malagasy species await description and a sixth species is known from Comoros. The genus can be distinguished from the sister genus *Sphyracephala* by the much reduced alula (Fig. 18), the presence of only one pair of scutal intra-alar setae (only in *C. sicardi* with an additional weak presutural seta), by wing vein *CuA+CuP* branching-off well before the apex of cell *cua* (Fig. 18) and by the moderate to high sexual dimorphy with regard to eye span. The eye stalks are longer and narrower than in Afrotropical *Sphyracephala*. Kotrba (2004) presented a phylogeny of the Diopsidae, based on cladistic analysis of morphological characters, in which *Cladodiopsis* was removed from Sphyracephalini and recovered as early branching in the Diopsini, although this was later retracted by Kotrba & Balke (2006), based on a combined morphological and molecular study. One species occurs almost at sea level, while other species occur in montane forests at elevations of 600–1,700 m.



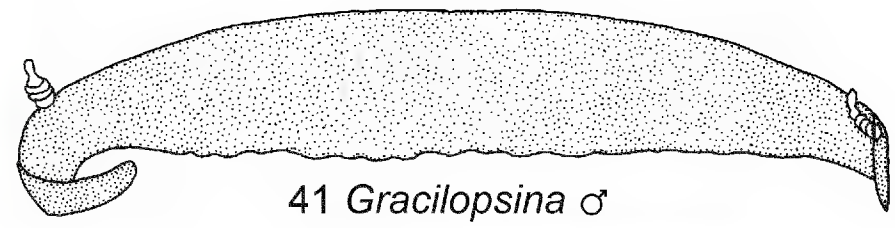
38 *Centrioncus* ♂



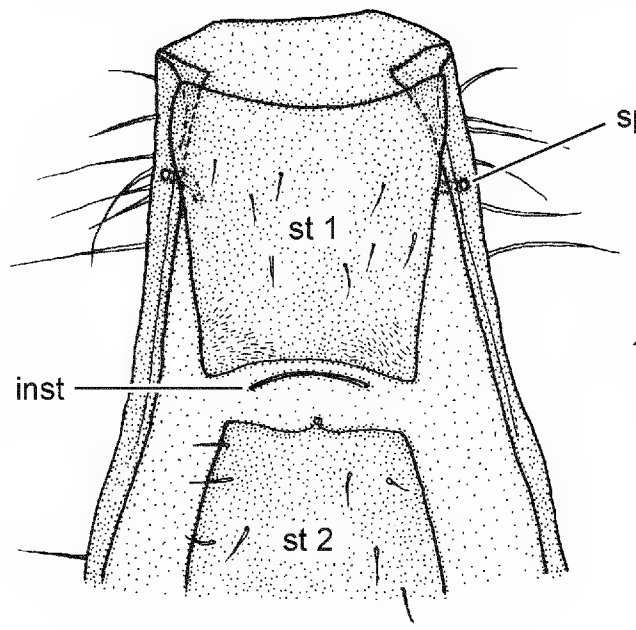
39 *Diopsina* ♂



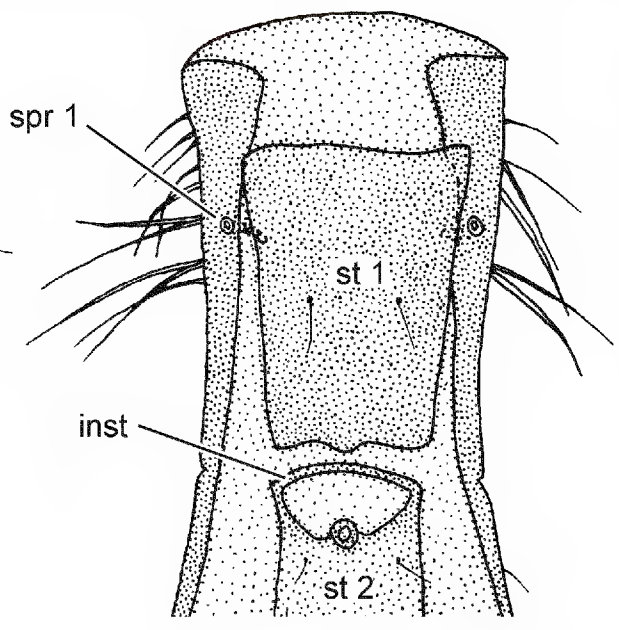
40 *Madagopsina* ♂



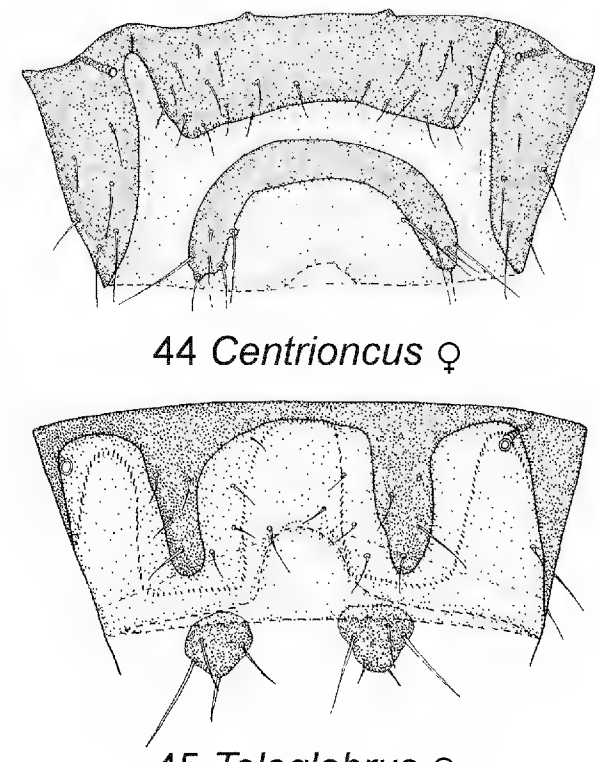
41 *Gracilopsina* ♂



42 *Madagopsina* ♀



43 *Gracilopsina* ♀



44 *Centrioncus* ♀

45 *Teloglabrus* ♀

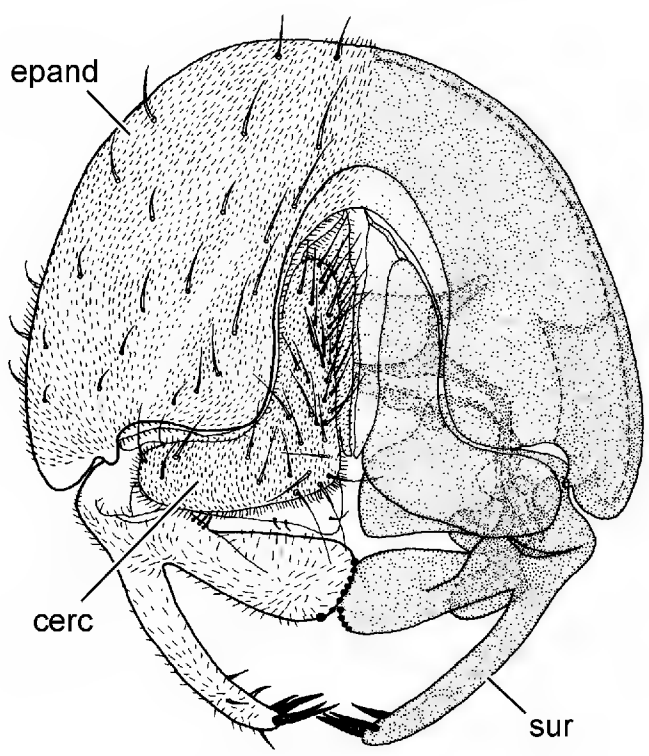
Figs 64.38–45. Abdominal features of Diopsidae: (38) male syntergosternite 7 + 8 of *Centrioncus aberrans* Feijen, ventral view; (39) same, *Diopsina fluegeli* Feijen & Feijen; (40) same, *Madagopsina freidbergi* Feijen, Feijen & Feijen, lateral view; (41) same, *Gracilopsina vadoni* (Vanschuytbroeck); (42) intersternite 1–2 of *M. apographica* (Séguy), ventral view ♀; (43) same, *G. vadoni* (Vanschuytbroeck); (44) female sternite 7 of *C. jacobae* Feijen, ventral view; (45) same, *Teloglabrus lebombensis* Feijen. Fig. 39 (Feijen & Feijen 2013, fig. 27), Figs 40–43 (Feijen *et al*. 2018, figs 70, 143, 21, 134, respectively), Figs 44, 45 (Feijen 1983, figs 31, 36).

Abbreviations: inst – intersternite; spr – spiracle; st – sternite.

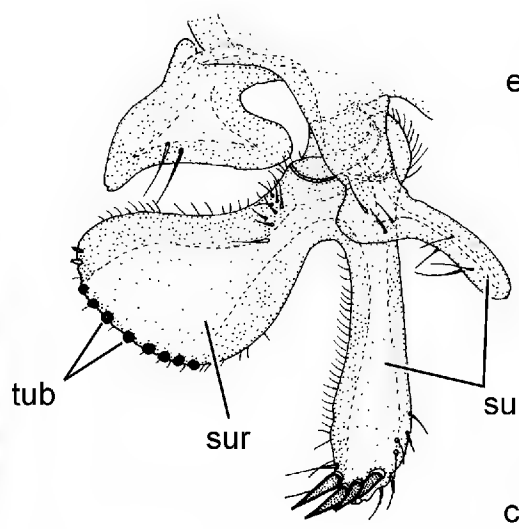
The immature stages have not been described. Séguy (1949) provided an ineffective identification key and the genus requires revision.

***Cobiopsis* Feijen** (Diopsinae)**.** An endemic monotypic genus (Fig. 8), with the single described species, *C. latifascia* (Brunetti, 1928). Other than the type series comprising two females from Sierra Leone, only one male is known from Nigeria. The genus belongs to the *Diasemopsis* genus-group and is characterised by the spinous outer vertical setae, the presence of intra-alar spines (Figs 8, 9), the large and laterally directed pleurotergal spines, the absence of scutal setae, the broad central wing band (Fig. 19) and an abdominal syntergite consisting of tergites 1–4. Biology and immature stages remain unknown.

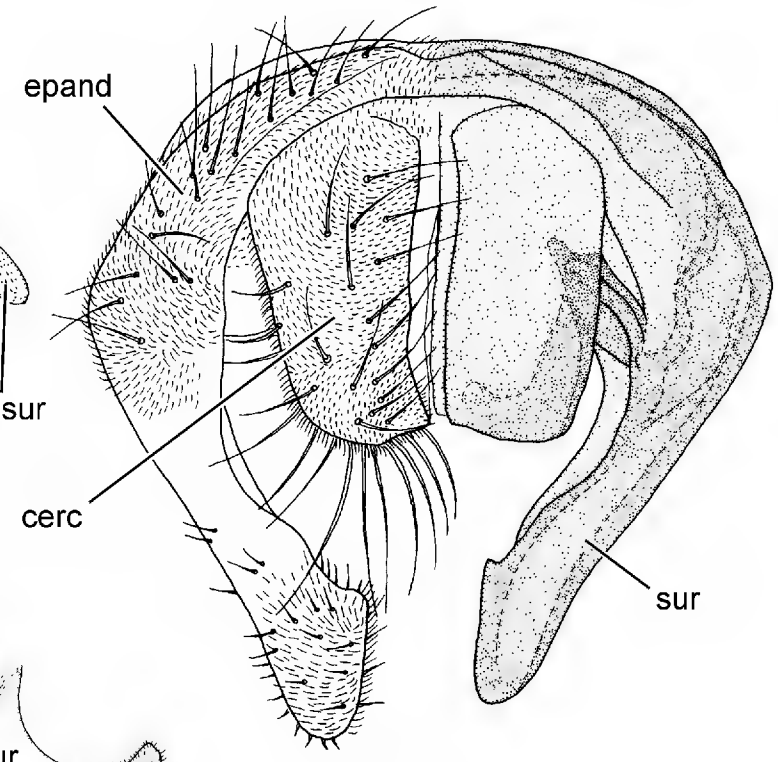
***Diasemopsis* Rondani** (Diopsinae)**.** An endemic genus of 46 described species, distributed in Central, East, Southern and West Africa, with one species extending into Yemen in the Southern Arabian Peninsula. About 100 species await description. *Diasemopsis* is by far the largest genus in the *Diasemopsis* genus-group. No proper diagnosis of the genus *Diasemopsis* exists. Most species have an intricate pattern of black and silvery-grey pruinescence on the abdomen (Fig. 33). The surstyli are seamlessly fused to the epandrium, the transition between spermatheca and duct is gradual and the abdomen is usually slender and apically pointed. Large concentrations of *Diasemopsis* occur in both rainforests and savanna habitats and all species are assumed to be saprophagous. Eggs of ten species were described by Meier & Hilger (2000), while the



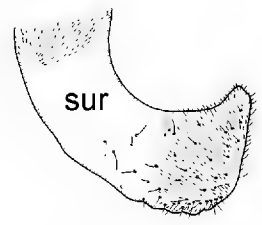
46 *Centrioncus* ♂



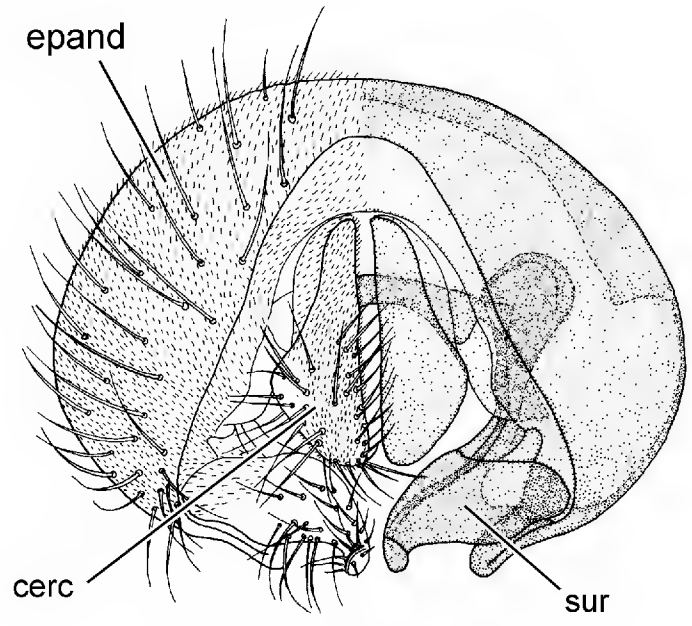
47 *Centrioncus* ♂



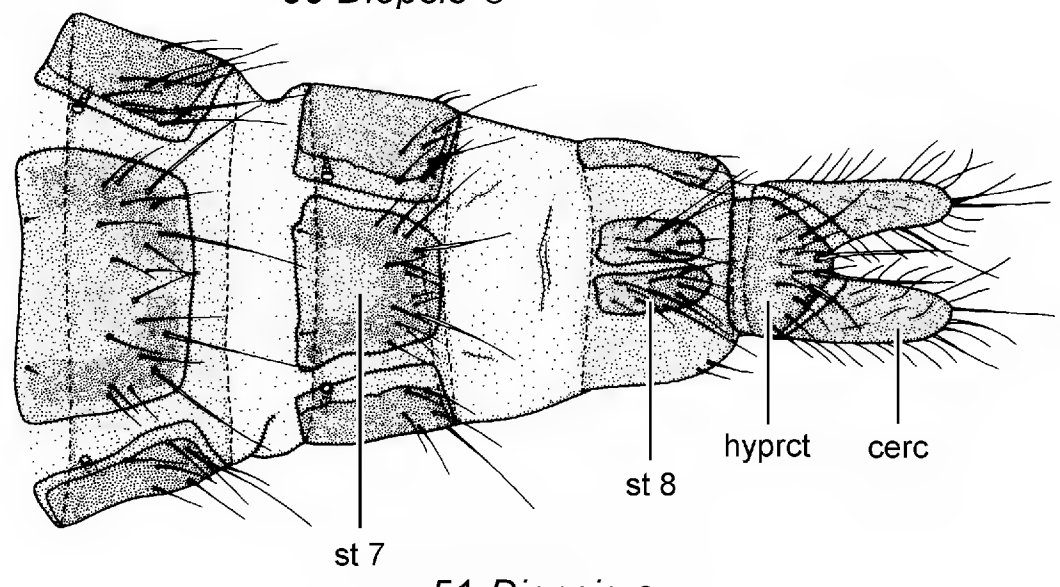
49 *Diopsis* ♂



50 *Diopsis* ♂



48 *Sphyracephala* ♂

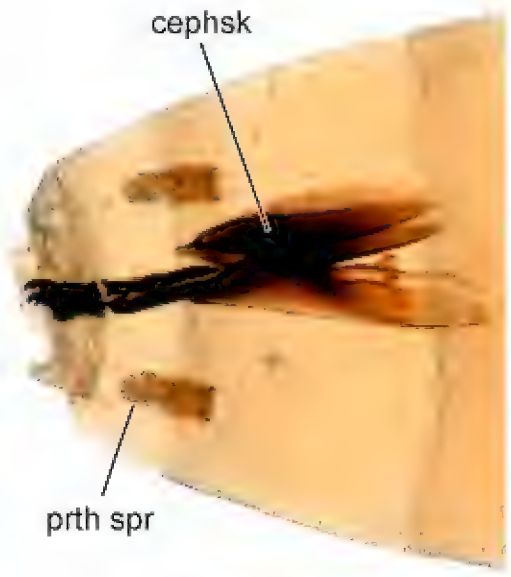


51 *Diopsis* ♀

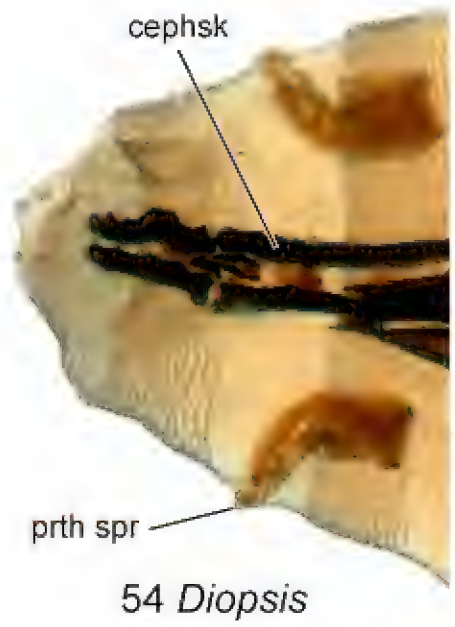
Figs 64.46–51. Male terminalia and female abdomen of Diopsidae: (46) male epandrium of *Centrioncus jacobae* Feijen, posterior view; (47) same, surstylus, inner view; (48) epandrium of *Sphyracephala beccarii* (Rondani), posterior view; (49) same, *Diopsis longicornis* Macquart; (50) same, surstylus, lateral view; (51) female abdomen of *D. stuckenbergi* Feijen & Feijen, ventral view. Figs 46, 47 (Feijen 1983, figs 67, 88), Fig. 51 (Feijen & Feijen 2012, fig. 24).

Abbreviations: cerc – cercus; epand – epandrium; hyprct – hypoproct; st – sternite; sur – surstylus; tub – tubercles.

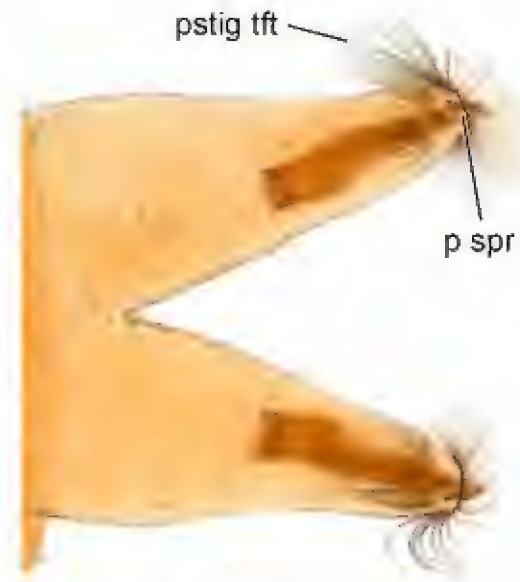
52 *Diopsis*



53 *Diopsis*

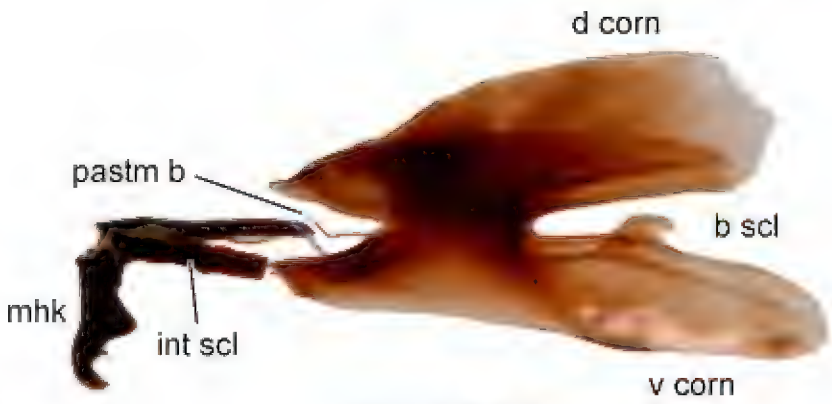


54 *Diopsis*



55 *Diopsis*

56 *Diopsis*



58 *Diopsis*

57 *Diopsis*

59 *Diopsis*

Figs 64.52–59. Immature stages of Diopsidae: (52) egg of *Diopsis longicornis* Macquart, lateral view; (53) same, larval pseudocephalon and prothorax, dorsolateral view; (54) same, ventral view; (55) same, larval posterior spiracles, dorsal view; (56) same, larval habitus, dorsal view; (57) same, prothoracic spiracles, dorsal view; (58) same, larval cephaloskeleton, lateral view; (59) same, puparium, dorsal view.

Abbreviations: b scl – basal sclerite; cephsk – cephaloskeleton; d corn – dorsal cornu; int scl – intermediate sclerite; mhk – mouthhook; p spr – posterior spiracle; pastm b – parastomal bar; prth spr – prothoracic spiracle; pstig tft – peristigmatic tuft; spr ppl – spiracular papilla; v corn – ventral cornu.

immature stages of two species were described by Descamps (1957: 39). Curran (1931) provided an identification key to 31 described species, but the genus requires revision.

***Diopsina* Curran** (Diopsinae)**.** An endemic genus of seven described species, distributed in Central, East, Southern and West Africa. A few additional species should be expected. The genus includes the smallest diopsids, ranging from 3.0–5.8 mm in length. They appear rather ant-like and in one species most individuals are brachypterous. Kotrba *et al*. (2010) discussed the phylogenetic position of the genus and Feijen *et al*. (2018), indicated that *Diopsina* is likely the sister-group of the Oriental genus *Eosiopsis*, based on a molecular analysis. The genus can be recognised by the deeper than long scutellum, the curved scutellar spines with pale base and tip and dark central section (Figs 35, 36), the irrorated dark wing (Fig. 20) and the strongly clavate abdomen, with small and equal-sized tergites 1 and 2, large and broad tergites 3 and 4 (Figs 35, 36) and sexual monomorphy with regards to eye span. The genus occurs along rivers or in swamps, mostly at or above 1,000 m elevation. Some species appear linked to clumps of bulrushes. The genus does not occur in rainforests. Biology and immature stages remain unknown. Feijen & Feijen (2013) attributed the seven species to the genus and provided an identification key.

***Diopsis* L.** (Diopsinae)**.** A genus of 68 described species (Fig. 1), occurring in the Afrotropical, Oriental and Palaearctic (Egypt and Palaearctic Saudi Arabia only) Regions. Currently, 62 species are recorded from the Afrotropics, distributed in Central, East, Southern and West Africa and in Madagascar. About 140 Afrotropical species await description, while in the Oriental *Diopsis indica* species-group another 20 new species should be expected. One species is recorded from Madagascar and three from Yemen in the Southern Arabian Peninsula (Feijen *et al*. 2017). Of these three species, *D. mayae* is an abundant species occurring from South Africa through East Africa to Egypt in the Palaearctic. A recent record extends the distribution of the genus as far as Greece (Anagnou-Veroniki *et al*. 2008), but this is likely an introduction into the rice fields. Two species of *Diopsis* were also found in Bhutan, a few kilometres from the border with the Palaearctic Region (H. Feijen, pers. obs.). The type genus of the Diopsidae was never formally re-described following Linnaeus' (1775: 5) original description of: head with stalks, eyes apically. Feijen & Feijen (2009) provided a provisional subdivision of *Diopsis* into nine species-groups, one of which includes Oriental *Diopsis*. These groups are not necessarily monophyletic, but do make this genus more accessible in the short term. Feijen & Feijen (2012) provided more information on the three Afrotropical species-groups, with a large apical wing macula. It remains to be seen whether the genus should be split into several genera. For the moment, *Diopsis* can be recognised by the presence of tiny or spinous inner vertical setae, the more or less straight scutellar spines without apical seta (Fig. 34), wing vein M_4 reaching margin (Figs 21–24) and abdominal syntergite 1–3 usually appearing as a single sclerite (Fig. 34). The genus exhibits the largest variation in wing pattern: uniformly clear or greyish; with large infuscated areas; with dark preapical or apical maculae; or with a very large central macula, with additional transverse bands (Figs 1, 21–24). *Diopsis* and *Eurydiopsis* are the only genera in which the apical scutellar seta is absent. *Diopsis* larvae exhibit a phytophagous (stem-boring), saprophytic, predatory or even cannibalistic way of life (Descamps 1957: 114; Feijen 1989: 42), with the ecology of Afrotropical stem-boring species relatively well-documented (Abu 1972: 10; Descamps 1957: 113; Feijen 1989: 58; Feijen & Schulten 1981; Scheibelreiter 1974). Eggs of six species were described by Meier & Hilger (2000), while the immature stages of eleven species were described by Descamps (1957: 33). Partial identification keys were provided by Feijen (1978), Lindner (1962) and Séguy (1955), but these keys are only of limited use, as the genus requires revision.

***Gracilopsina* Feijen, Feijen & Feijen** (Diopsinae)**.** An endemic genus of two described species: *G. sinespina* Feijen, Feijen & Feijen, 2018 and *G. vadoni* (Vanschuytbroeck, 1965), confined to Madagascar (Feijen *et al*. 2018). Given the large number of Malagasy diopsids studied, it is unlikely that additional species will be discovered, but given the rareness of *Gracilopsina* it is possible. This genus was recently erected (together with *Madagopsina*) in a revision of Malagasy diopsids with irrorated wings. Both genera are endemics to Madagascar and were earlier included in *Eurydiopsis* Séguy & Vanschuytbroeck *nec* Frey. Species were earlier alternately placed in *Cyrtodiopsis*, *Diopsis*, or *Eurydiopsis* and even in *Teleopsis*, if accepting this genus as senior synonym of *Cyrtodiopsis*, as proposed by Meier & Baker (2002). Feijen (2011), however, elaborated why the synonymy of *Cyrtodiopsis* with *Teleopsis* should be rejected. Feijen *et al*. (2018) provide detailed information on the earlier generic assignments of the species now included in *Gracilopsina* and *Madagopsina*. *Gracilopsina*, for which no molecular data are yet available, is not necessarily the sister-group of *Madagopsina*. *Gracilopsina* can be recognised by the dark colouration (Fig. 7), the distinct inner vertical setae, the presence of a precoxal bridge (Fig. 15), the irrorated wing (Fig. 25), the weak apical scutellar setae, the very slender syntergite with distinct seam between tergites 2 and 3, with intersternite 1–2 linked to main sternite 2 (Fig. 43), the surstyli without an apophysis and fused to epandrium and the moderate to high dimorphy with regard to eye span. Very little is known about the ecology of the genus. The photographed *G. sinespina* (Fig. 7), occurred on a *Pandanus* species (Pandanaceae) in the eastern part of Madagascar at an elevation of *ca* 1,000 m and *G. vadoni* is only known from the north-eastern forests of Madagascar at elevations of 10–200 m. The eggs of both species were described by Feijen *et al*. (2018), but other immature stages remain unknown. An identification key to the two species was provided by Feijen *et al*. (2018).

***Madagopsina* Feijen, Feijen & Feijen** (Diopsinae)**.** An endemic genus of five described species confined to Madagascar, with one additional species awaiting description. *Madagopsina* is the second Malagasy genus recently described and its history and phylogenetic placement was already discussed under *Gracilopsina* (above). Feijen *et al*. (2018) discussed the results of molecular analysis for two of the species. *Madagopsina* was placed in the group of Diopsidae with irrorated wings and tentatively as the sister-group to Oriental *Eurydiopsis* (based on nuclear markers only). The genus is characterised by a peculiar yellowish brown colour (Fig. 6), the distinct inner vertical setae, presence of basiliform prosternum (Fig. 14), the irrorated wing (Fig. 26), the weak apical scutellar setae, the slender syntergite with distinct seam between tergites 2 and 3 (Fig. 37), intersternite 1–2 not linked to main sternite 2 (Fig. 42), the articulated surstyli with a strong apophysis and low to moderate sexual dimorphy with regard to eye span. Two species occur in the northern forests of Madagascar, one species in the western forests and two in the eastern regions (one also extending into the

north). The western species occurs at elevations between 130 and 820 m, while the other species occur at elevations varying between 300 and 1,100 m. The eggs of two species were described in Feijen *et al*. (2018), but other immature stages remain unknown. *Madagopsina apographica* (Séguy, 1949) has remarkably large eggs of 2.0 mm. An identification key to the five species was provided by Feijen *et al*. (2018).

***Sphyracephala* Say** (Sphyracephalinae)**.** A genus of 10 described species (Fig. 4), occurring in the Afrotropical, Australasian, Nearctic, Oriental and Palaearctic Regions. Two species are recorded from the Afrotropics: *S. beccarii* (Rondani, 1873) (Fig. 4), recorded from Central, East, Southern and West Africa, Madagascar, Oman, United Arab Emirates and Yemen in the Afrotropics and in Palaearctic Algeria and Saudi Arabia and *S. munroi* Curran, 1928, from Central, East, Southern and West Africa. Additional species are not expected from the region. The genus was briefly reviewed by Feijen (1989: 66), but a European species was subsequently discovered by Papp *et al*. (1997). *Sphyracephala* are small diopsids (3.5–6.0 mm), with usually short, stout eye stalks (Fig. 4) and two pairs of scutal setae. The wing has a well-developed alula (Fig. 27) and the apical scutellar setae are more than three times the scutellar spine length. Afrotropical species occur along rocky riverbeds, but can disperse in the rainy season. Among Diopsidae, clustering of flies is most pronounced in *Sphyracephala* (Feijen *et al*. 2017). Eggs of *S. beccarii* were described by Meier & Hilger (2000), while all immature stages of this species were described by Descamps (1957: 41). Collart (1954) provided a table listing the differences between the two Afrotropical species.

***Teloglabrus* Feijen** (Centrioncinae)**.** An endemic genus of 15 described species (Fig. 3), distributed in Mozambique, South Africa, Swaziland and Zimbabwe. A few additional species should be expected from the region. This genus was erected for the stalkless Diopsidae occurring south of the Zambezi River. It is sometimes placed in synonymy with *Centrioncus* (McAlpine 1997a). Molecular analyses have so far only dealt with *Teloglabrus*, not with *Centrioncus*, and thus do not serve to resolve the issue. It is noteworthy that differences between various *Teloglabrus* species are greater than in *Centrioncus*. The genus can be distinguished from *Centrioncus* by its usually yellow palpus, the absence of a central wing macula and presence of distal fasciae on the hind femur in most species, the male terminalia with a narrow, bell-shaped epandrium with ratio width/length 1.0–1.3, the glabrous outer and median arms of the surstylus, the normal-sized ejaculatory apodeme and the female sternite 7 with two anterior sclerites narrowly connected on the meson anteriorly (Fig. 45) and two posteriorly positioned small sclerites (this pair lost in some species). All species occur in rainforest, with the exception of *T. stuckenbergi* Feijen, 1983, which occurs above the rainforest zone. The eggs were described by Feijen (1983) and Meier & Hilger (2000), but the other immature stages have not been described. Feijen (1983) provided an identification key to species.

***Trichodiopsis* Séguy** (Diopsinae)**.** An endemic genus of five described species, distributed in Central and West Africa. At least seven additional undescribed species are known, including one from eastern Kenya. Séguy (1955) erected this genus for *T. minuta* Séguy, 1949 and provided a short diagnosis which gives little support to distinguish the genus from *Diasemopsis*. Séguy's identification key (1955: 1103), however, gave the apparent reasons for distinguishing the new genus as: curved scutellar spines without apical seta, body clothed in long, erect setulae, no facial teeth. Séguy placed *Trichodiopsis* close to *Cyrtodiopsis*. At generic level, however, the characters mentioned by Séguy are weak, while *Trichodiopsis* can simply not be placed near *Cyrtodiopsis* as they belong to different genus-groups. *Trichodiopsis minuta* definitely has an apical scutellar seta (as in Fig. 11), as do all *Diasemopsis*, while strong setulosity occurs in a number of *Diasemopsis* species. There are other reasons to separate *Trichodiopsis* from *Diasemopsis*, such as the large, bare (non-microtrichose) areas of wing (Fig. 28), the strong, erect, inner vertical and intra-alar setae, both often on cones or tubercles (Figs 11, 12), the weak, but distinct, basal constriction of the second abdominal segment and the small size. Feijen (1989: 63) referred *D. exquisita* Brunetti, 1928 and *D. pulchella* Eggers, 1916 to *Trichodiopsis*. In addition to the type species of the genus (*T. minuta*), *D. horni* Curran, 1931 and *D. quadrata* Curran 1931 are also included in *Trichodiopsis*. *Diasemopsis albifacies* Curran, 1931 is recognised as junior synonym of *T. exquisita*, while *D. interrupta* is a junior synonym of *T. pulchella*. Eggs of *T. exquisita* (as *Diasemopsis albifacies*) were described by Meier & Hilger (2000), but other immature stages have not been described. An identification key is not available.

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PSILIDAE 65

(Rust Flies or Psilid Flies)

Anatole I. Shatalkin

Fig. 65.1. Male of *Loxocera* sp. (Madagascar) (photograph © S.A. Marshall).

Diagnosis

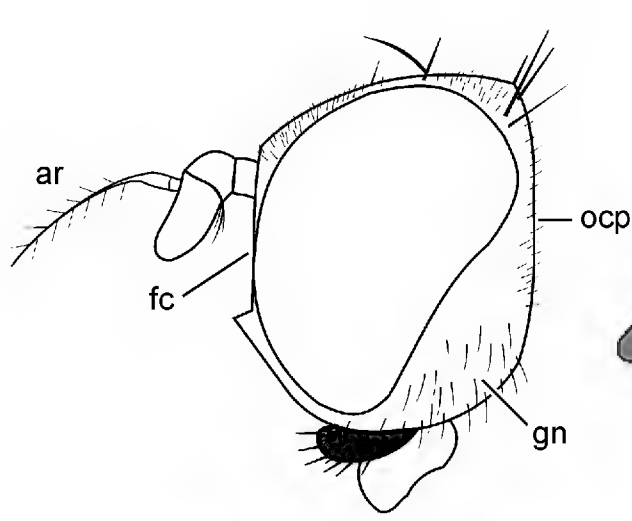
Small- to medium-sized (body length: 2.5 mm (in Psilini) to 13 mm (some Loxocerini)), black or yellow acalyptrate flies, clearly diagnosed externally on wing venation (peculiar costagial break (Figs 13, 14), subcostal vein (*Sc*) incomplete (Fig. 14), straight vein *CuA* closing distal margin of cell *cua*) (Fig. 13), reduced setation (0–1 notopleural setae, humeral, posthumeral and usually acrostichal setae absent, pleuron without setae) and form of head and body.

Head (Figs 2–8) rather wide (viewed in profile), spherical to hemispherical (owing to flat occiput) in Chylizinae (Fig. 2) and *Belobackenbardia* Shatalkin (Fig. 8), or triangular with projecting frons and receding face in most Psilinae (Fig. 7); face in *Chyliza* Fallén concave below antennae, forming angle at fore margin of subcranial cavity (Fig. 2); frons flat and wide in both sexes; ocellar triangle usually small in *Chyliza*, enlarged in non-Afrotropical *Psila* Meigen, sometimes virtually reaching anterior margin of frons; frontal vitta sclerotised, subshiny (de-sclerotised and usually velvety in some non-Afrotropical Loxocerini); occiput swollen (*Loxocerosoma* Verbeke, Figs 4, 5; Psilini, Fig. 7), more or less straight (in Afrotropical *Loxocera* Meigen) or slightly concave (*Chyliza*, Fig. 2); gena narrow (*Belobackenbardia*, Fig. 8 and *Chyliza*, Fig. 2), or broad, sometimes very broad (some *Loxocera* and Psilini, Figs 3, 6, 7); parafacial (viewed from above) with silvery pruinosity (*Belobackenbardia* and *Chyliza*); *Belobackenbardia* characterised

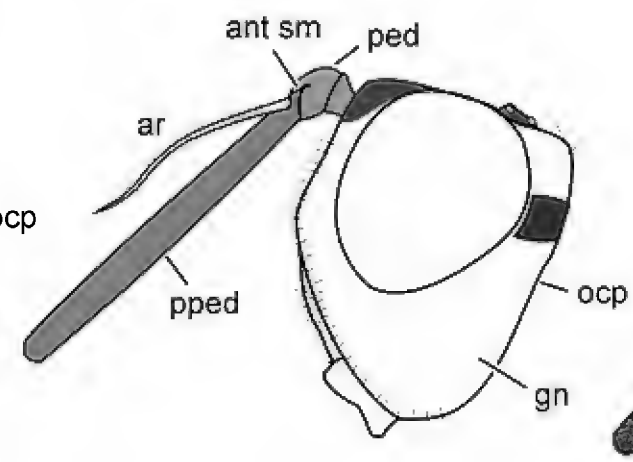
Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2021. Manual of Afrotropical Diptera. Volume 3. Brachycera—Cyclorrhapha, excluding Calyptratae. *Suricata* 8. South African National Biodiversity Institute, Pretoria; pp. 1545–1556.

by peculiar genal patch of short, white pile situated some distance from hind margin of eye along concave margin (Fig. 8); in *Chyliza* similar brush of shorter white pile extends as narrow fascia directly along margin of eye (genal patch also occurs in two allied species of *Loxocera*, the European *L. aristata* (Panzer, 1801) and Oriental *L. glandicula* Iwasa, 1993, but the parafacial lacks dense silvery macrotrichia); compound eyes dichoptic in both sexes, round or oval, with sloping, concave (*Belobackenbardia*, Fig. 8), or slightly convex (*Chyliza*, Fig. 2) hind margin; antenna elbowed, short to long; pedicel with dorsal antennal seam; in *Loxocera* and *Loxocerosoma* (Figs 3, 4) postpedicel greatly lengthened, usually longer than face; arista brown, yellowish brown or white, slender, or as an exception, thick (*Chyliza*, subgenus *Dasyna* Robineau-Desvoidy), with short or long setulae; proboscis short; palpus small, narrow in Psilinae and leaf-like in *Chyliza*; head setation complete in *Chamaepsila* Hendel (Fig. 6), including divergent postocellar setae (reduced in some genera), 2 pairs of vertical setae (outer vertical seta duplicated in many *Chamaepsila* and *Chyliza*), 0–2 pairs of short fronto-orbital setae; ocellar triangle with 2 long, divergent ocellar setae (Fig. 6); in Afrotropical species of *Loxocera* and *Loxocerosoma psiloides* Verbeke, 1968, ocellar setae underdeveloped, often setula-like; vertical and postocellar setae weak, but in some Madagascan species (Fig. 4) these setae well-developed; vibrissa absent in all Psilidae.

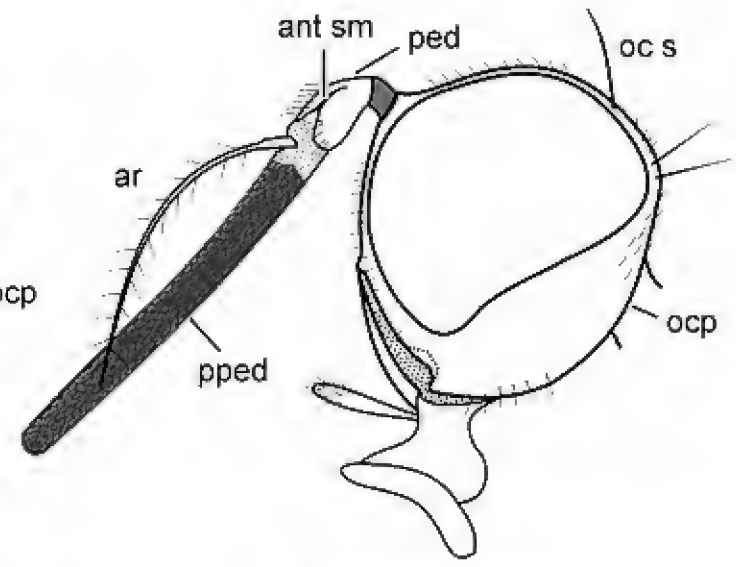
Thorax of usual proportions, elongate (most Psilini), or truncated in comparison with abdomen (most Loxocerini); prosternum weakly sclerotised; katatergite enlarged, callus-like in *Chyliza* (which also differ by presence of well-developed postmetacoxal bridge); mesonotum (Fig. 10) with 0–1 pair of notopleural setae; 0–6 pairs of dorsocentral setae; acrostichal setae usually not differentiated (*Chyliza* and some species of Palaearctic *Chamaepsila hebraica*-group with 1 prescutellar pair); 0–1 pair of supra-alar setae, 1 pair of postalar setae, 1–3 pairs of scutellar setae; pleuron without differentiated setae; katepisternum ventrally with large seta in front of mesocoxa in *Belobackenbardia* (Fig. 9); anepisternum in ventral part with peculiar bunch of white, ventrally directed setulae in



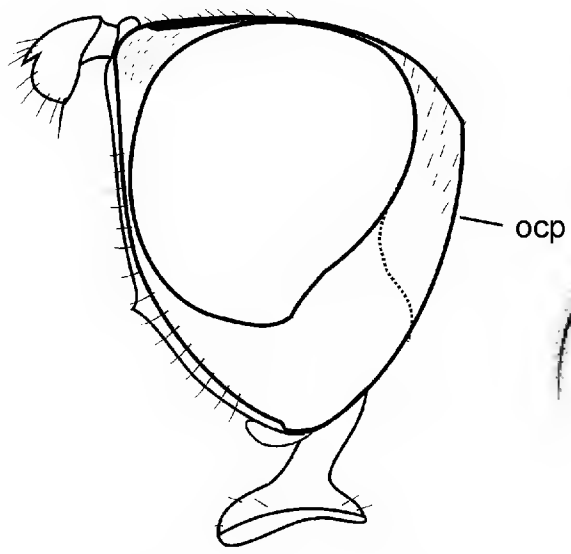
2 *Chyliza*



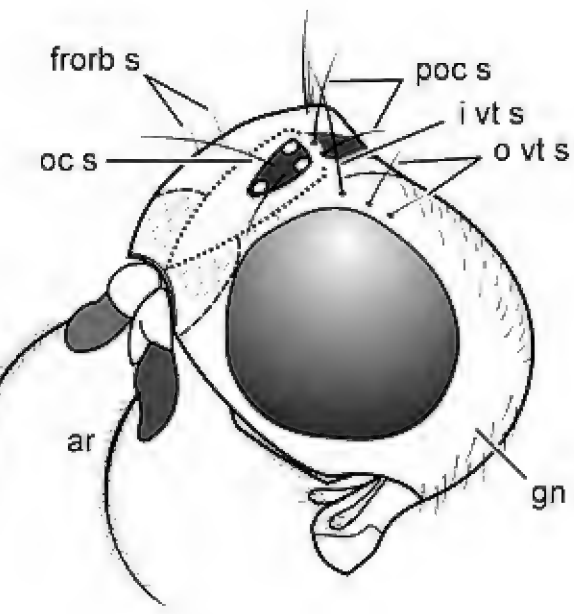
3 *Loxocera*



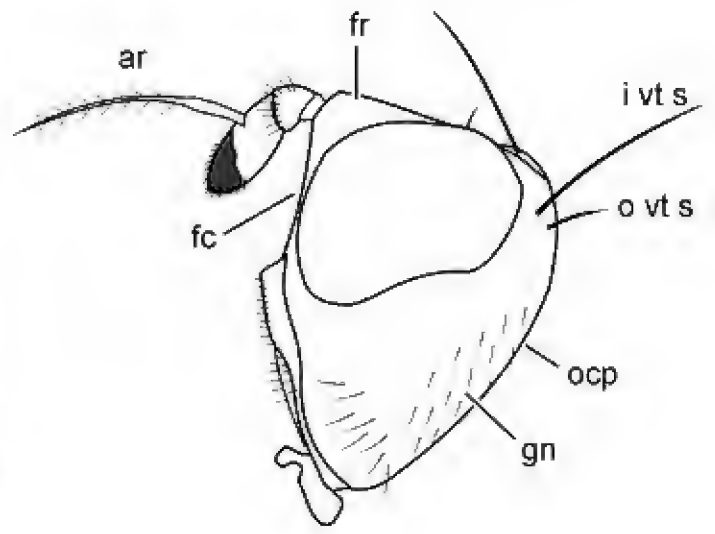
4 *Loxocerosoma*



5 *Loxocerosoma*



6 *Chamaepsila*

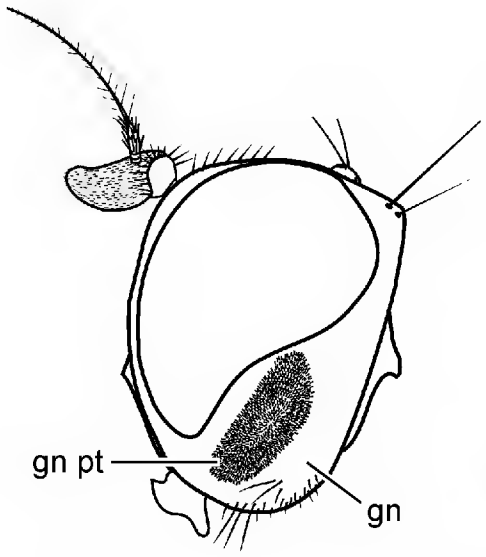


7 *Afropsila*

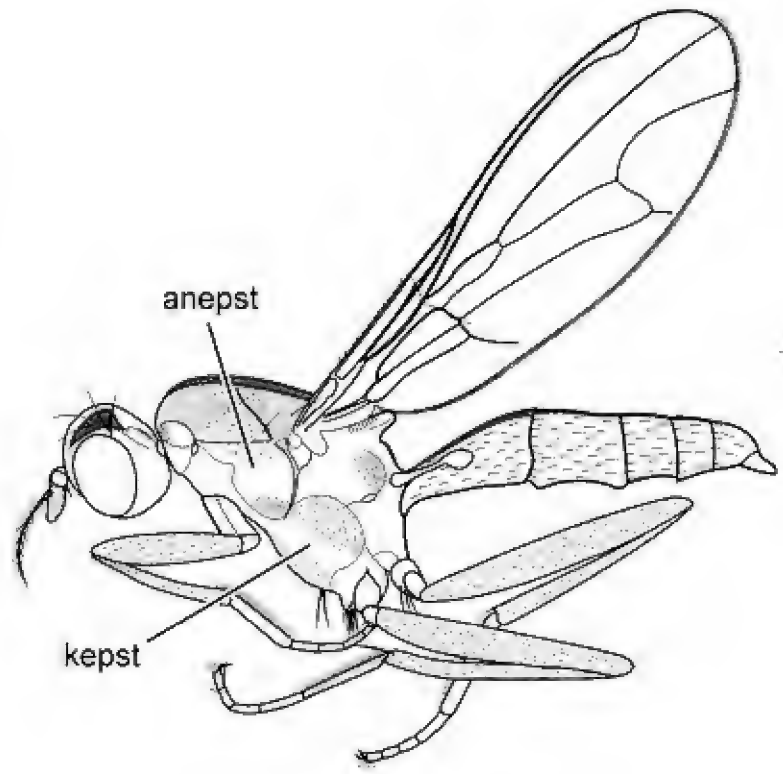
Figs 65.2–7. Heads of Psilidae (lateral views): (2) *Chyliza latifrons* Verbeke; (3) *Loxocera dispar* Bezzi; (4) *Loxocerosoma glabra* (Verbeke); (5) *L. psiloides* Verbeke (postpedicel and arista omitted); (6) *Chamaepsila aethiopica* (Verbeke); (7) *Afropsila dimorpha* (Verbeke).

Abbreviations: ant sm – antennal seam; ar – arista; fc – face; fr – frons; frorb s – fronto-orbital seta; gn – gena; i vt s – inner vertical seta; o vt s – outer vertical setae; oc s – ocellar seta; ocp – occiput; ped – pedicel; poc s – postocellar seta; pped – postpedicel.

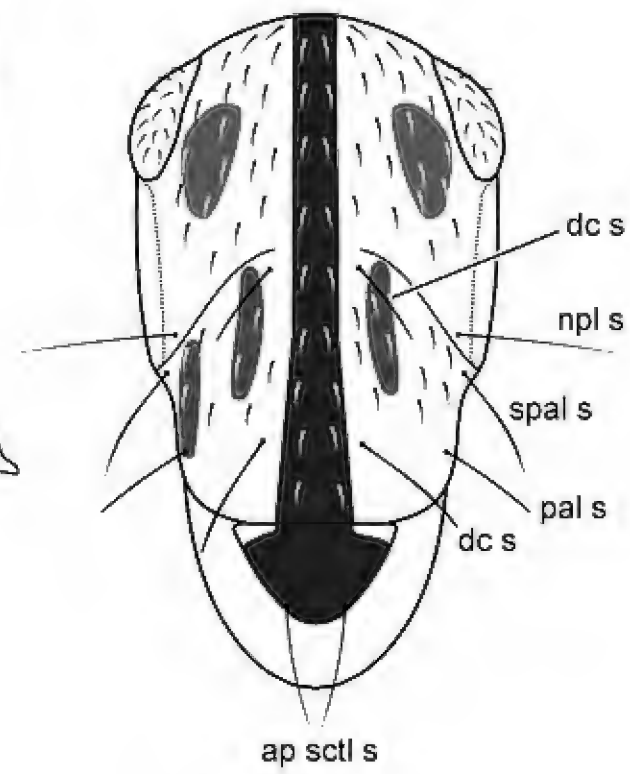
Belobackenbardia (Fig. 9), in *Chyliza* and *Loxocera*, these setulae well-distinguished from shorter dorsally directed setulae on dorsal part of anepisternum; katepisternum bearing similar white setulae on virtually entire surface of sclerite in *Chyliza*, but only dorsal part in *Belobackenbardia*; anepimeron bare, without delicate setulae in Afrotropical Psilidae. Wing membrane hyaline, often yellowish or brownish tinted in apical ½, less often with brown apical macula (in some *Chyliza*), or with faint brownish central area, sometimes divided into two areas; without contrasting maculae and fascia on veins in Afrotropical Psilini; costal vein (*C*) with broad subcostal break at level of distal end of subcostal vein; subcostal vein (*Sc*) incomplete, not reaching costal vein (*C*); base of wing with narrow wavy flexion line (Figs 13, 14) extending from subcostal break to posterior end of basal medial cell (*bm*) and crossing crossvein *m–cu* near apex of basal medial cell (*bm*); veins R_1 and *Rs* weakened at point of crossing; appearing as break in some cases; in some *Chyliza* wavy flexion line between subcostal break and vein R_1 entirely devoid of microtrichia; in other cases this line bearing microtrichia, but these distinctly shorter than surrounding wing microtrichia; cell *cua* closed, with vein *CuA* straight; cell *cua* virtually as long as basal medial cell (Psilinae; Fig. 14) or distinctly shorter (*Chyliza*; Fig. 13); vein *CuA+CuP* not reaching wing margin; alula clothed in microtrichia in Afrotropical Psilidae; halter whitish to yellow, with knob blackish in *Afropsila* Shatalkin females. Legs slender; male fore and sometimes mid tibiae with anteroventral comb of black spinules in basal ⅓ or ½ (*Chyliza*; absent in *Dasyna*); male fore femur of *Chyliza sepsoides* Verbeke, 1952 with spinules in apical ⅓ (Fig. 12); hind femur sub-apically with shallow, microtrichose, oval ventral pit in *Chyliza* (Buck 2010, fig. 60.5); hind femur near apex with ventral brush of short (6–10 × shorter than width of femur),



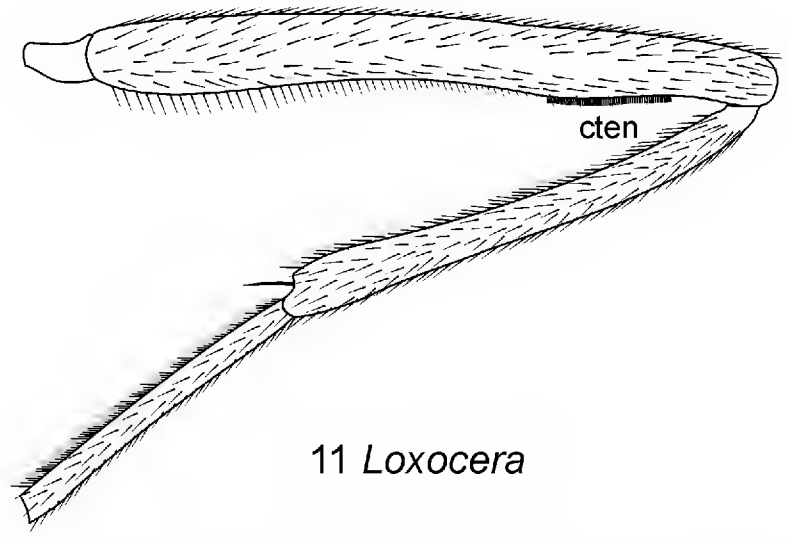
8 *Belobackenbardia*



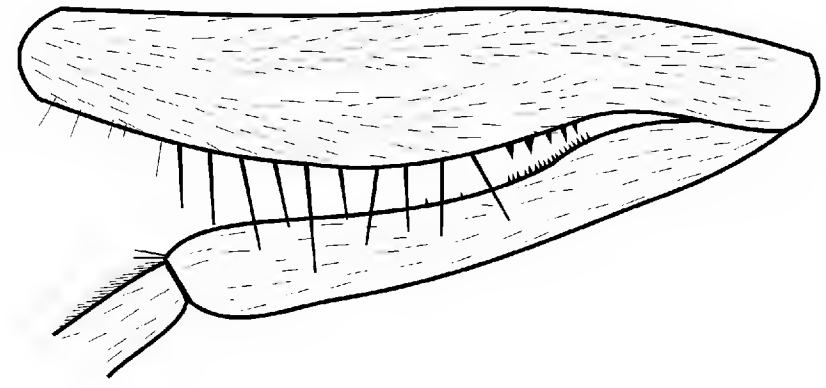
9 *Belobackenbardia*



10 *Chamaepsila*



11 *Loxocera*



12 *Chyliza*

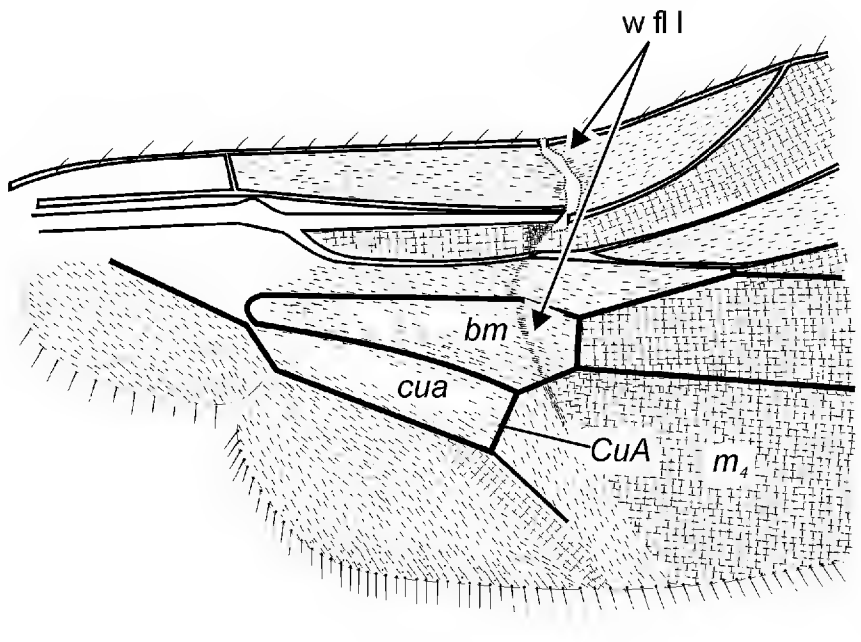
Figs 65.8–12. Head, habitus, mesonotum and legs of Psilidae: (8) head of *Belobackenbardia cornicula* Shatalkin, lateral view ♂; (9) same, habitus, lateral view; (10) mesonotum of *Chamaepsila aethiopica* (Verbecke), dorsal view; (11) hind femur and tibia of *Loxocera rufa* Loew, lateral view; (12) fore femur and tibia of *Chyliza sepsoides* Verbeke, lateral view.

Abbreviations: anepst – anepisternum; ap sctl s – apical scutellar seta; cten – ctenidium; dc s – dorsocentral seta; gn – gena; gn pt – genal patch; kepst – katepisternum; npl s – notopleural seta; pal s – postalar seta; spal s – supra-alar seta.

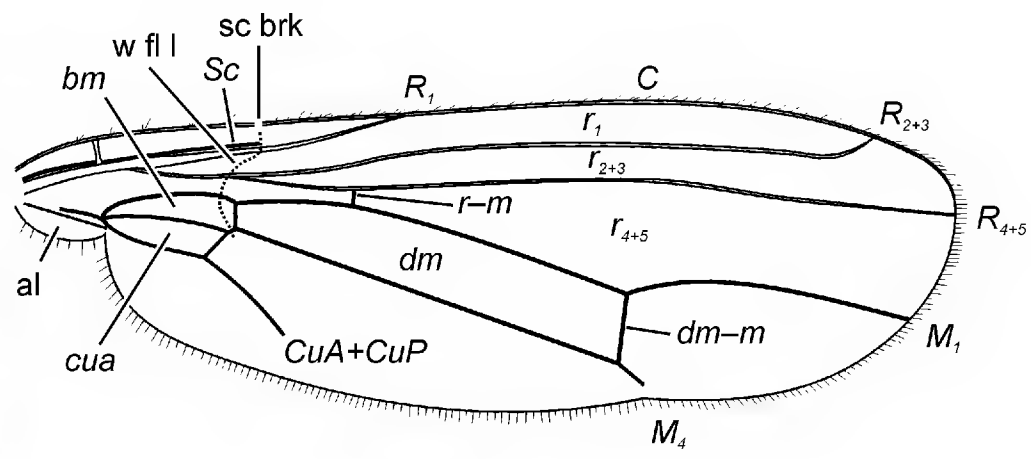
white standing pile (felt-like microtomentum; Buck & Marshal 2006*b*) in both sexes of *Loxocera* (Fig. 11).

Abdomen oval to elongate (in *Loxocera*), without strong setae; male tergite and sternite 6 well-developed, with regular pattern of sternal spinules in *Chyliza* (Fig. 15); abdominal spiracle 7 absent in females, present or absent in males (Hennig 1973: 52; McAlpine 1989: 1434); dorsal pregenital sclerite absent (Chylizinae) or present (Psilinae) (Buck 2010); male terminalia exhibit 3 basic types of structures: *Chyliza* (Figs 15–18) differ from Psilinae in having epandrium with well-developed surstyli; subepandrial sclerite (bacilliform sclerite) well-developed; hypandrium forming ring-like structure extended in dorsoventral plane, each side in ventral ⅓ with long appendage (hypandrial apodeme); distiphallus often transformed to complex structure bearing pair of lobes (Figs 16, 17); in Afrotropical *Chyliza* postgonites (parameres of authors) well-developed (Figs 17, 18), or reduced to weak formations (Fig. 16); phallapodeme resembles bent rod which curves ventrally in caudal ⅓ and connects with hypandrium by unsclerotised ligament (Figs 16, 18); in Psilinae surstyli absent; in Afrotropical *Loxocera* lateral margins of epandrium become lamellar, extended, turning up ventrally, often entirely closing hypandrial complex (Fig. 19); phallus T-shaped (Figs 20, 21); subepandrial sclerite reduced, in form of 2 small plates between phallus and epandrium, often distinguished; postgonites well-developed; phallapodeme (Fig. 22) as in *Chyliza*, not fused with hypandrium, as in Holarctic *Imantimyia* Frey; hypandrium may be shortened on mid-line (Fig. 20) up to its division into two lateral sclerites, as in *Loxocerosoma* (Fig. 23); in *Chamaepsila* (Fig. 25) hypandrium secondarily subdivided into unpaired ventral plate (hypandrium proper = sternite 9) and pair of lateral sclerites, which may correspond to derivatives of gonopods (Iwasa 1998: 180, fig. 6); in *Afropsila* (Figs 26–28) hypandrium proper absent; phallus broad, with sclerotised basal capsule (basiphallus) supporting tubular apical portion of distiphallus (Fig. 28); in *Belobackenbardia* (Figs 29–32) epandrium massive in comparison with hypandrium; apical forked lobes being practically continuation of epandrium, may be homologous with surstyli; hypandrium U-shaped; pair of lateral sclerites (Figs 30–32) each side between hypandrium and epandrium may correspond to derivatives of gonopods (Shatalkin 2002); phallus upcurved (with primitive dorsal orientation – Griffiths 1972: 37), with pair of lateral ribbon-like lobes (postgonites?); female postabdomen with ovipositor soft, weakly sclerotised in *Chyliza* and Psilini (except European *Psilosoma* Zetterstedt); in Afrotropical *Chamaepsila* and *Chyliza,* epiproct (dorsal sclerite), hypoproct (ventral sclerite) and cerci not fused with each other (Figs 33–35); in *Chyliza* segments 7 and 8 desclerotised, sternite 8 poorly discerned, forming small plate; in Afrotropical *Loxocera* the proctiger forms very long cone (Figs 36, 37), distinctly longer than segment 8, drawn into abdomen at rest (Fig. 38); cerci not distinguished, possibly fused with epiproct; in *Belobackenbardia* ovipositor massive, segment 8 with weakly sclerotised tergite and sternite, narrowed caudally (Shatalkin 2002, fig. 8); spermathecae unsclerotised in Psilidae (Hennig 1973: 53).

Egg elliptical or cylindrical, whitish to yellowish brown in colour (some *Loxocera*), length: 0.6–2.3 mm, width: 0.18–0.35 mm (Buck & Marshall 2006*b*; Gaponov 1999); micropylar pole simple (*Loxocera*), or with 6–10 (8 in *Chamaepsila rosae* (F., 1794)) large respiratory crypts (crevices) surrounding and rising above micropyle in form of cap (Psilini), or with corona of small, club-shaped processes (*Chyliza*); chorion sculptured with network of lamellate polygonal ridges (*Chyliza*), or by coarse longitudinal ridges, sometimes connected by low, transverse ridges (Psilini); in *Loxocera* surface without ridges, or with fine low polygonal or longitudinal ridges.



13 *Chyliza*



14 *Chamaepsila*

Figs 65.13–14. Wings of Psilidae: (13) basal portion of wing of *Chyliza rwindiensis* Verbeke, dorsal view; (14) wing of *Chamaepsila aethiopica* (Verbeke), dorsal view.

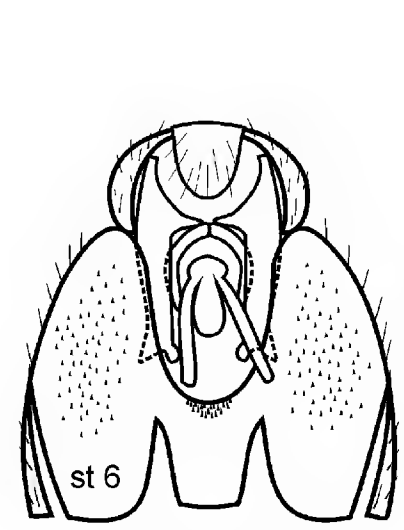
Abbreviations: al – alula; *bm* – basal medial cell; *C* – costal vein; *CuA* – anterior branch of cubital vein; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *dm* – discal medial cell; *dm–m* – discal medial crossvein; M_1 – first branch of media; M_4 – fourth branch of media; m_4 – fourth medial cell; R_1 – anterior branch of radius; r_1 – first radial cell; R_{2+3} – second branch of radius; r_{2+3} – second radial cell; R_{4+5} – third branch of radius; r_{4+5} – third radial cell; *r–m* – radial–medial crossvein; *Sc* – subcostal vein; sc brk – subcostal break; w fl l – wavy flexion line.

Larvae slender and smooth; in *Chamaepsila rosae* third-instar larva (Fig. 41) 6–7 mm in length, yellowish red in colour (if carrot-fed), or white (if turnip or white root-fed); anterior end pointed, bearing cephaloskeleton (Fig. 39), with basal and intermediate sclerites partially fused (in larvae of other species these sclerites may be free); facial mask above the oral opening with system of four types of sensilla (Fig. 42): ampullacea (= coeloconica), basiconica, campaniform and styloconica (Ryan & Behan 1973); prothoracic spiracle (Fig. 43) located on fleshy base bearing 5–6 finger-like papillae (Figs 42, 43); form of prothoracic spiracle similar in *Chamaepsila nigricornis* (Meigen, 1826) (Fig. 44), but *Synaphopsila nartshukae* Shatalkin, 1986 (Iwasa 1998: 181) and *Chyliza* (Ferrar 1987: 786) with 13–15 papillae; segment 8 with pair of well-developed, dark posterior spiracles elevated above surface of segment; with 3 spiracular openings, elongate-oval, often lying at approximate right angles to one another (Fig. 40).

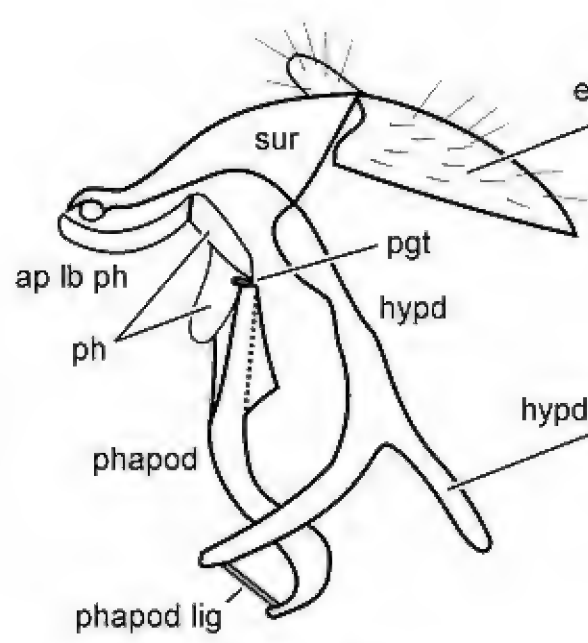
Most adult Psilidae are not easily confused with flies of other families, even in the wild, although some species of the tribe Psilini superficially resemble Chloropidae (see Chapter 96); most Psilinae are well-diagnosed by the triangular head with a receding face.

Biology and immature stages

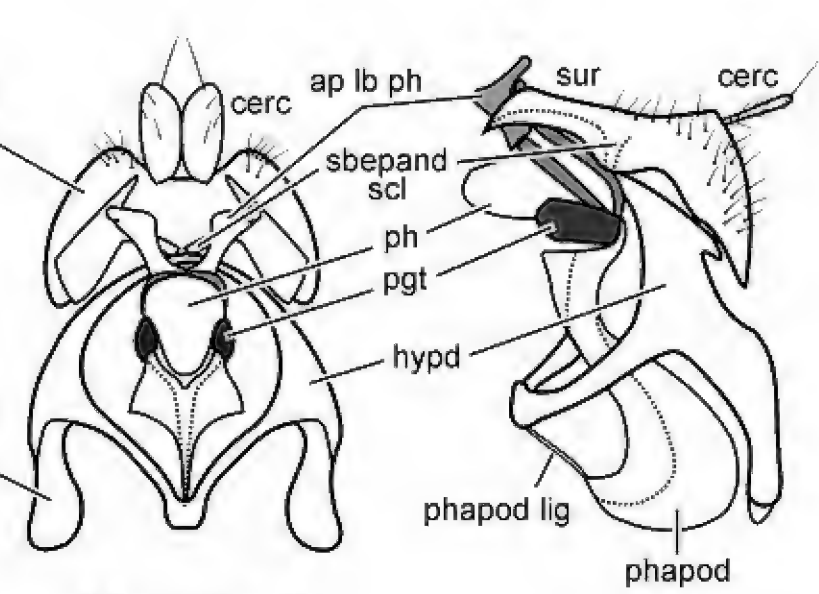
Adult psilids occur on low vegetation in shaded situations and adults are frequently observed resting on foliage or may occur on flowers. Some species prefer open situations, such as waste areas with weeds, meadows and marshes.



15 *Chyliza* ♂

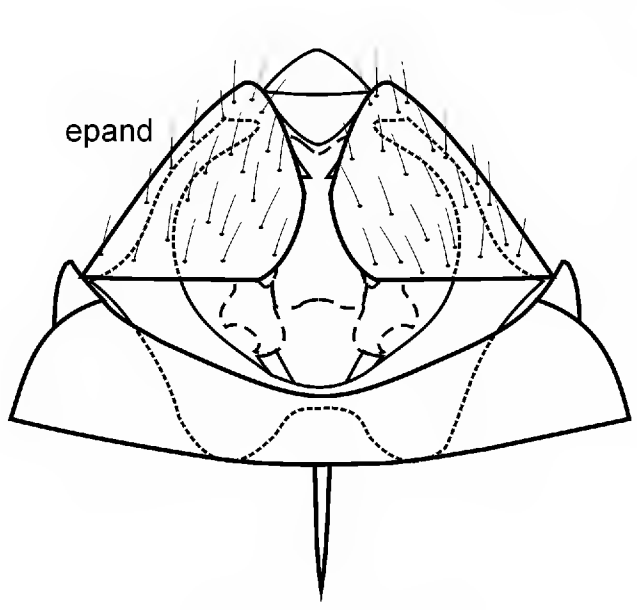


16 *Chyliza* ♂

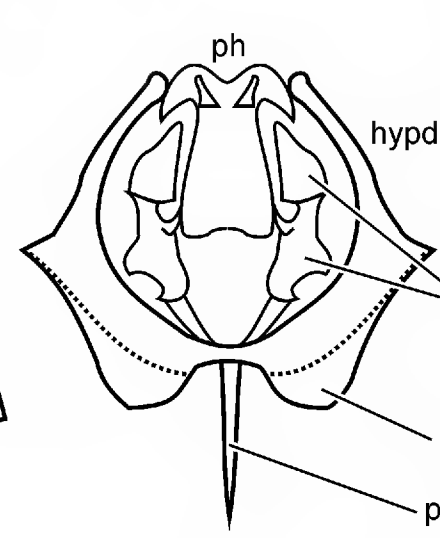


17 *Chyliza* ♂

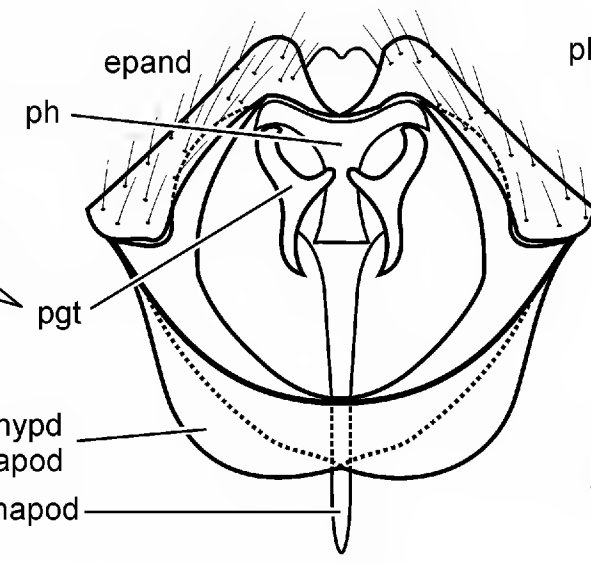
18 *Chyliza* ♂



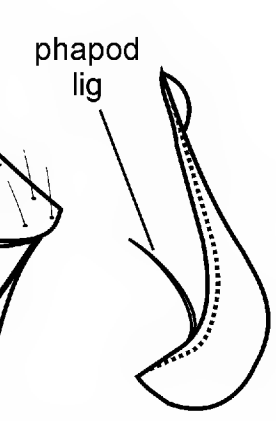
19 *Loxocera* ♂



20 *Loxocera* ♂



21 *Loxocera* ♂



22 *Loxocera* ♂

Figs 65.15–22. Male terminalia of Psilidae: (15) sternite 6 and terminalia of *Chyliza rwindiensis* Verbeke, ventral view; (16) same, terminalia, lateral view; (17) terminalia of *Ch. hackarsi* Verbeke, caudoventral view; (18) same, lateral view; (19) postabdomen of *Loxocera macrogramma* Speiser, ventral view; (20) same, hypandrium and associated structures, ventral view; (21) terminalia of *L. pilipleura* Verbeke, ventral view (lateral margins of epandrium teased apart and turned caudally); (22) same, phallapodeme, lateral view.

Abbreviations: ap lb ph – apical lobe of phallus; cerc – cercus; epand – epandrium; hypd – hypandrium; hypd apod – hypandrial apodeme; pgt – postgonite; ph – phallus; phapod – phallapodeme; phapod lig – ligament connecting phallapodeme with hypandrium; sbepand scl – subepandrial sclerite; st – sternite; sur – surstylus.

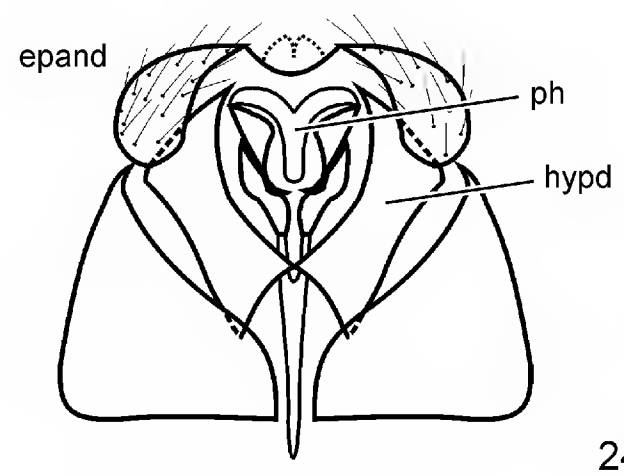
Larvae of Psilidae are phytophagous, burrowing into stems, roots and tubers, or beneath the bark of living trees. Larvae of the Palaearctic species *Chyliza leptogaster* (Panzer, 1798) are known to cause phloem necroses in deciduous trees (Dengler 1997) and larvae of *Ch. annulipes* Macquart, 1835, have been recorded on conifers, particularly in resinous wounds (Lyneborg 1987). *Chyliza vittata* Meigen, 1826, is noted as a miner pest in stems and roots of Orchidaceae (De Meijere 1940; Petit 1982) and larvae of *Ch. bambusae* Yang & Wang, 1988 occur in the roots of bamboo (Poaceae) (Yang & Wang 1988). *Chyliza splendida* Iwasa, 1989 feeds on galls induced by *Asphondylia baca* Monzen, 1937 (Diptera: Cecidomyiidae) in Japan (Sugiura & Yamazaki 2006). Larvae of *Ch. leptogaster* and some endemic Oriental species of *Chyliza* cause galls on thin twigs of bushes, e.g., *Spiraea* spp. (Rosaceae). Larvae of the Nearctic *Ch. leguminicola* Melander, 1920 occur presumably in stalks or roots of *Lupinus polyphyllus* Lindl. (Fabaceae). The known species of Loxocerini develop in stems of sedges (Cyperaceae) (Chandler 1975; De Meijere 1941; Ferrar 1987: 300).

Little is known about the immature stages of Afrotropical psilids. Parker & Riches (1993: 131) indicate the occurrence of a *Psila* species larva in the stems of *Orobanche minor* Smith (Orobanchaceae) in Ethiopia, but it is not clear from their account whether flies were reared from larvae or were determined based on larvae alone. As *Psila* (*sensu stricto*) is restricted to Eurasia and does not occur in the Afrotropical Region, only *Afropsila* or *Chamaepsila* can here be implied. The larva is described as up to 1 cm in length, and thus appears too large for species of these genera. As far as is known, only one species, the Broomrape root-fly, *Chyliza* (*Dasyna*) *extenuata* (Rossi, 1790), is recorded on plants of this genus. Its larvae form galls on underground stems of Broomrape, *Orobanche* spp. (Chandler 1975). The two species of *Dasyna* are only recorded from the Palaearctic Region.

Eggs of Psilidae have been described by Gaponov (1999), Buck (2010: 840) and Buck & Marshall (2006*a*, *b*). Buck (2010: 841) provided an illustrated key to eggs of Psilidae genera.

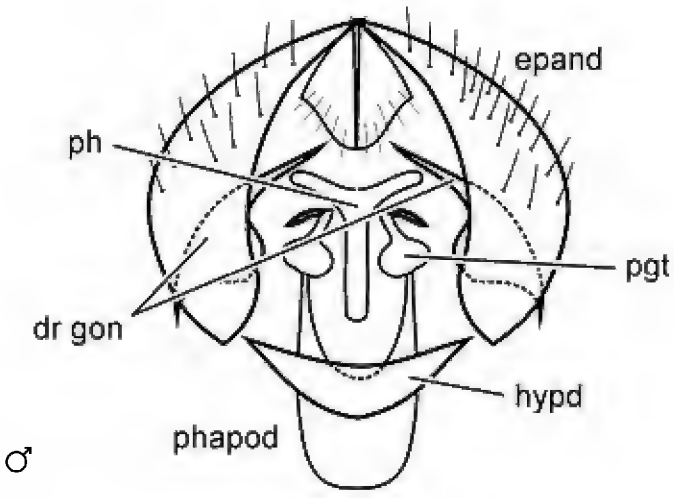
Economic significance

Relatively few psilids are recorded as crop pests. Larvae of the Carrot (rust) fly, *Chamaepsila rosae*, causes considerable damage to cultivated carrots and other root crops, as well as

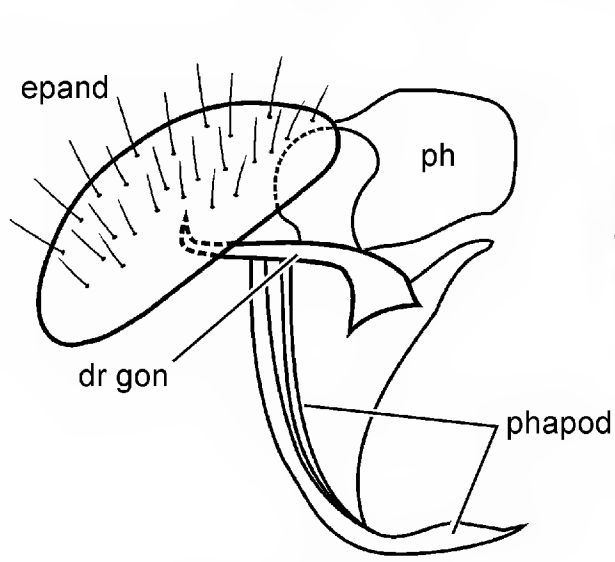


23 *Loxocerosoma* ♂

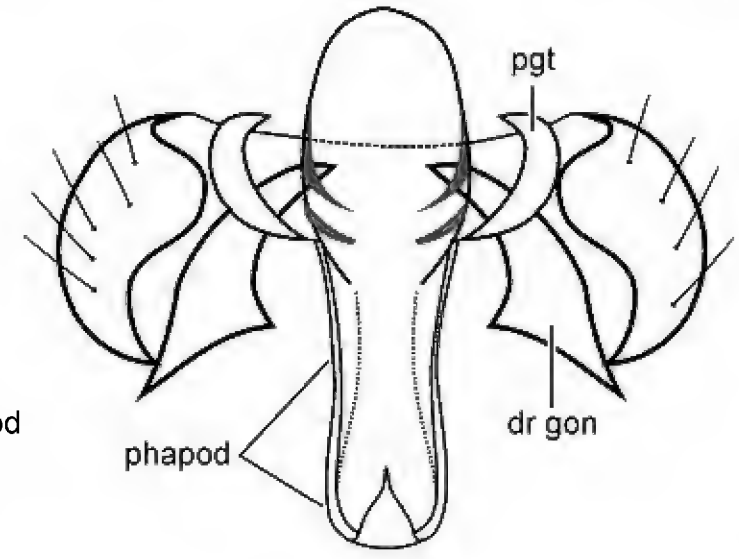
24 *Loxocerosoma* ♂



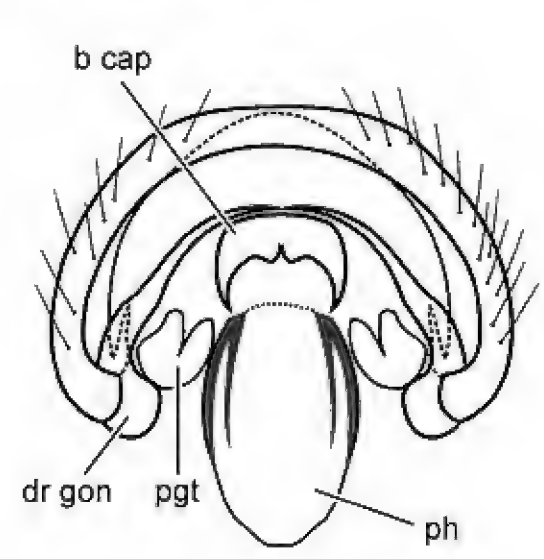
25 *Chamaepsila* ♂



26 *Afropsila* ♂



27 *Afropsila* ♂



28 *Afropsila* ♂

Figs 65.23–28. Male terminalia of Psilidae: (23) sternite 6 and terminalia of *Loxocerosoma seyrigi* (Verbeke), ventral view; (24) same, postgonite, lateral view; (25) terminalia of *Chamaepsila aethiopica* (Verbeke), caudal view; (26) terminalia of *Afropsila dimorpha* (Verbeke), lateral view; (27) same, caudoventral view; (28) same, caudal view.

Abbreviations: b cap – basal capsule of phallus; dr gon – derivative of gonopod; epand – epandrium; hypd – hypandrium; pgt – postgonite; ph – phallus; phapod – phallapodeme.

wild Apiaceae and Asteraceae; 121 host species have been recorded (Ellis *et al*. 1992). Adult flies are characterised by the black body, but are termed "Carrot (rust) fly", due to the rust-coloured frass left by tunnelling larvae in stored root crops. The species is registered in South Africa as a pest of carrots and parsnips and is likely introduced. In Japan *Synaphopsila nartshukae* is a severe pest of carrots (Iwasa *et al*. 1987). Some species, including *Chamaepsila nigricornis* (Meigen, 1826) and *C. bicolor* (Meigen, 1826), are also registered as root pests of cultivated Asteraceae flower crops (Glendenning 1952; Osborne 1955; Vernon 1962), and if occurrence of the former Palaearctic species in Kenya is confirmed (Shatalkin 2002), then this would also likely represent human-facilitated introduction.

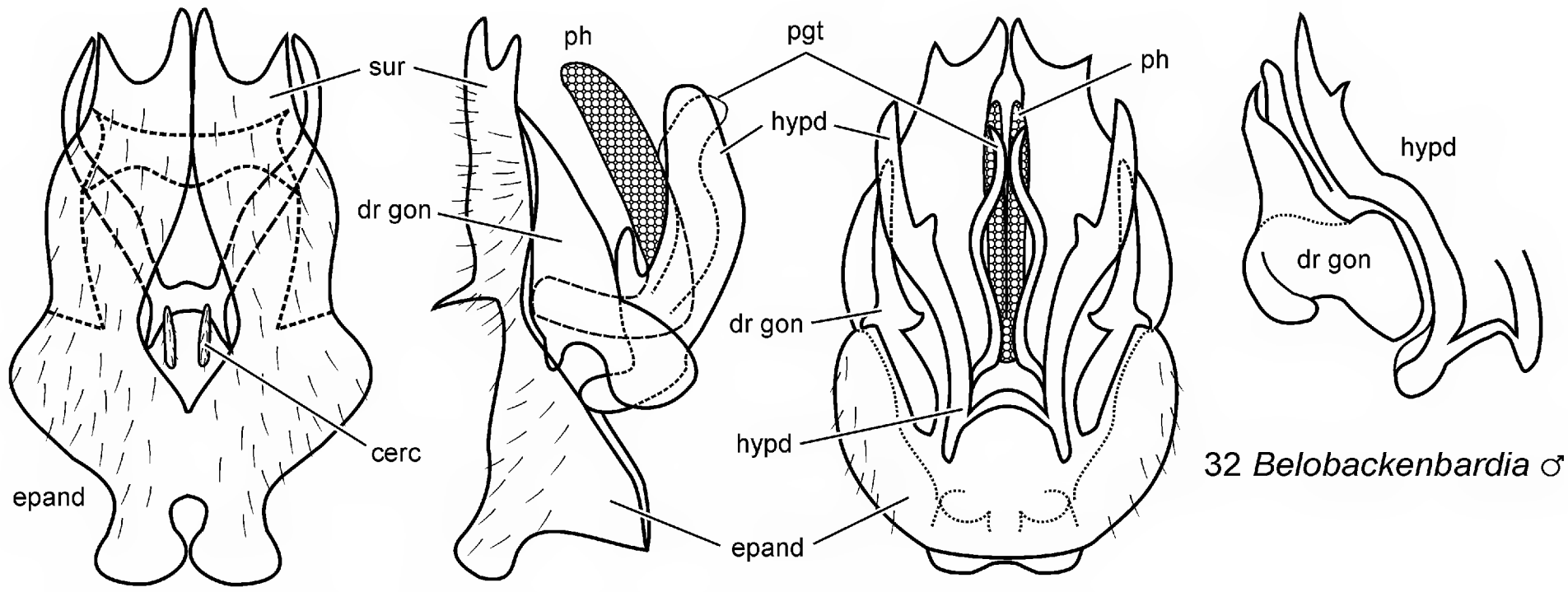
Classification

Most authors follow Hennig (1971, 1973: 53) and McAlpine (1989: 1432), in including Psilidae in the superfamily Diopsoidea (Nothyboidea). Both these authors considered the Neotropical family Somatiidae as the closest relative of Psilidae and also placed in Diopsoidea the families Syringogastridae, Tanypezidae, Megamerinidae, Nothybidae (all non-Afrotropical) and Diopsidae. McAlpine (1997) excluded Somatiidae, Tanypezidae and Megamerinidae from the Diopsoidea.

Traditionally, the family has been divided into two subfamilies: the plesiomorphic Chylizinae and the more derived Psilinae (Cogan 1980: 589; Iwasa 1998: 179; Steyskal 1987: 782). More recently, a third subfamily, Belobackenbardiinae, was recognised, comprising only the relic genus *Belobackenbardia* (3 species) from South Africa (Shatalkin 2002). Unlike the two other subfamilies, the terminalia structure of *Belobackenbardia* exhibits a more primitive condition (upcurved phallus). There are no synapomorphies indicating monophyly of *Belobackenbardia* + *Chyliza* and all character states connecting these two genera (genal patch of short, white pile; parafacial silvery pruinose; katepisternum and anepisternum with group of white, ventrally directed setulae) are plesiomorphic (McAlpine 1997). The perceived primitive condition of the male terminalia of *Belobackenbardia* is possibly secondarily a result of morphological reversion. Sister-group relationships between these subfamilies cannot be established at present. The Chylizinae, with the single genus *Chyliza*, includes 118 described species and has a global distribution.

The subfamily Psilinae is divided into two tribes: Loxocerini (55 described species globally, not including *Asiopsila* Shatalkin) and Psilini (164 species globally, including *Asiopsila*). The limits of the Loxocerini, traditionally defined by the shared character of a lengthened postpedicel were recently revised. The subgenus *Asiopsila* was established for Oriental species of *Loxocera* and Buck & Marshall (2006*b*) have convincingly argued that *Asiopsila* represents a group within Psilini. Afrotropical *Loxocera* apparently form a monophyletic group, differing from the rest of the Loxocerini in head form and terminalia structure.

Species of Psilini are grouped into several monophyletic groups, considered by some authors as valid genera (Hennig 1941: 11; Soós 1984: 28), and by others as subgenera of *Psila sensu lato* (Cogan 1980: 589; Iwasa 1998: 180; Shatalkin 1989); some groups are not recognised by authors as separate taxa. The number, composition, taxonomic position, relationships and history of their study were reviewed by Shatalkin & Merz (2010). Phylogenetic relationships of the monophyletic groups within Psilini are, however, not yet fully resolved and require further study. Hennig (1965) described the fossil genus and species *Electrochyliza succini* Hennig, 1965 from Baltic Amber, considered here as a stem-group of Chylizinae + Psilinae.



29 *Belobackenbardia* ♂ 30 *Belobackenbardia* ♂ 31 *Belobackenbardia* ♂

Figs 65.29–32. Male terminalia of Psilidae: (29) *Belobackenbardia cornicula* Shatalkin, dorsal view; (30) same, lateral view; (31) same, ventral view; (32) same, right derivative of gonopod and hypandrium (part), ventrolateral view.

Abbreviations: cerc – cercus; dr gon – derivative of gonopod; epand – epandrium; hypd – hypandrium; pgt – postgonite; ph – phallus; sur – surstylus.

Identification

The Afrotropical Psilidae fauna has not been revised recently. The identification keys to Palaearctic (Hennig 1941: 9; Iwasa 1998: 180) and Nearctic (Steyskal 1987: 782) genera are of limited use, given that these exclude some endemic Afrotropical genera (*Afropsila*, *Belobackenbardia* and *Loxocerosoma*). Afrotropical psilids of these genera are easily identified in the field, based on external characters. Identification of species presents difficulties given incomplete knowledge of the Afrotropical fauna. Many species await description and known species require re-examination and revision. Verbeke's identification keys are outdated and lack several species described by him and others. Species identification of Psilinae is largely based on colour characters and chaetotaxy. Species of *Chyliza* are difficult to identify and requires the examination of male terminalia. Psilidae are best micro-pinned in the field for later double-mounting (see Chapter 2).

Key to genera of Afrotropical Psilidae

1. Thorax with postmetacoxal bridge; katatergite enlarged, callus-like; wing cell *cua* distinctly shorter than basal medial cell (*bm*) (Fig. 13); hind femur with tomentose pit on ventral sub-apical surface (CHYLIZINAE) . . . . . *Chyliza* Fallén
– Thorax without postmetacoxal bridge; katatergite not enlarged, bare or with very short pile; wing cell *cua* subequal in length to basal medial cell (*bm*) (e.g., Fig. 14); hind femur with ventral sub-apical region unmodified or with brush of dense pile (e.g., Fig. 11) 2
2. Gena of head with well-developed oval patch of short, white pile posterior to compound eye (Fig. 8); parafacial (viewed from above) silvery pruinose; pleuron with distinct setae; katepisternum ventrally with large black seta in front of mesocoxa and in upper portion with patch of white, ventrally directed hair-like setulae (Fig. 9) (BELOBACKENBARDIINAE) . . . . . *Belobackenbardia* Shatalkin
– Gena of head without patch of short, white pile; parafacial (viewed from above) without silver pruinosity; pleuron without distinct setae; katepisternum without ventrally directed white setulae (PSILINAE) . . . 3
3. Antennal postpedicel greatly elongate and parallel-sided, antennae appearing distinctly longer than face (e.g., Figs 3, 4); hind femur with ventral ctenidium of very dense, short, whitish pile preapically (e.g., Fig. 11); thorax with anepisternum with group of white, ventrally directed hair-like setulae in lower part (LOXOCERINI) 4
– Antennal postpedicel short, not parallel-sided, antennae appearing shorter than face (e.g., Figs 6, 7); hind femur without ctenidium of dense pile; thorax with anepisternum without bunch of ventrally directed setulae in lower part (PSILINI) 5
4. Head with occiput flat (Fig. 3); male terminalia with lateral sides of epandrium lamellar, turned ventrad, partially or entirely covering hypandrial complex (Fig. 19); hypandrium with ventral hypandrial apodemes well-developed (Figs 20, 21) . . . . . *Loxocera* Meigen
– Head with occiput clearly convex (Figs 4, 5); male terminalia with lateral sides of epandrium unmodified, not lamellar, nor abutting each other ventrally; hypandrium (Fig. 23) without ventral plate . . . . . *Loxocerosoma* Verbeke
5. Antennal arista and setulae brownish or yellow; thorax with well-developed postalar and notopleural seta; wing with halter yellow in both sexes; male terminalia with ventral plate of hypandrium; phallus T-shaped (Fig. 25) . . . . . *Chamaepsila* Hendel
– Antennal arista white (narrowly yellow basally), with short white setulae; thorax without postalar seta, notopleural seta weak; wing with halter yellow in male and blackish in female; male terminalia without ventral plate of hypandrium; phallus tubular, with basal sclerotised capsule (Figs 26–28) . . . . . *Afropsila* Shatalkin

Synopsis of the fauna

The family Psilidae comprises 340 described species of which 52, belonging to five genera, occur in the Afrotropical Region.

***Afropsila* Shatalkin** (Psilinae: Psilini)**.** A monotypic genus, with the single species, *A. dimorpha* (Verbeke, 1956), described from Rwanda and further recorded from Cameroon, Kenya, Tanzania and Uganda. The species was originally included in the genus *Psila* (*sensu stricto*), but Cogan (1980: 590) placed it in the subgenus *Chamaepsila*, possibly following examination of specimens with well-developed postocellar setae. This character, dividing *Psila* and *Chamaepsila*, is variable in *A. dimorpha*. *Psila* (*Tetrapsila*) *longipennis* (Séguy, 1936) from the Azores Is. resembles *A. dimorpha* externally, and coupled with the presence of black halteres in females, indicates that this species may also belong in *Afropsila*. The biology and immature stages remain unknown.

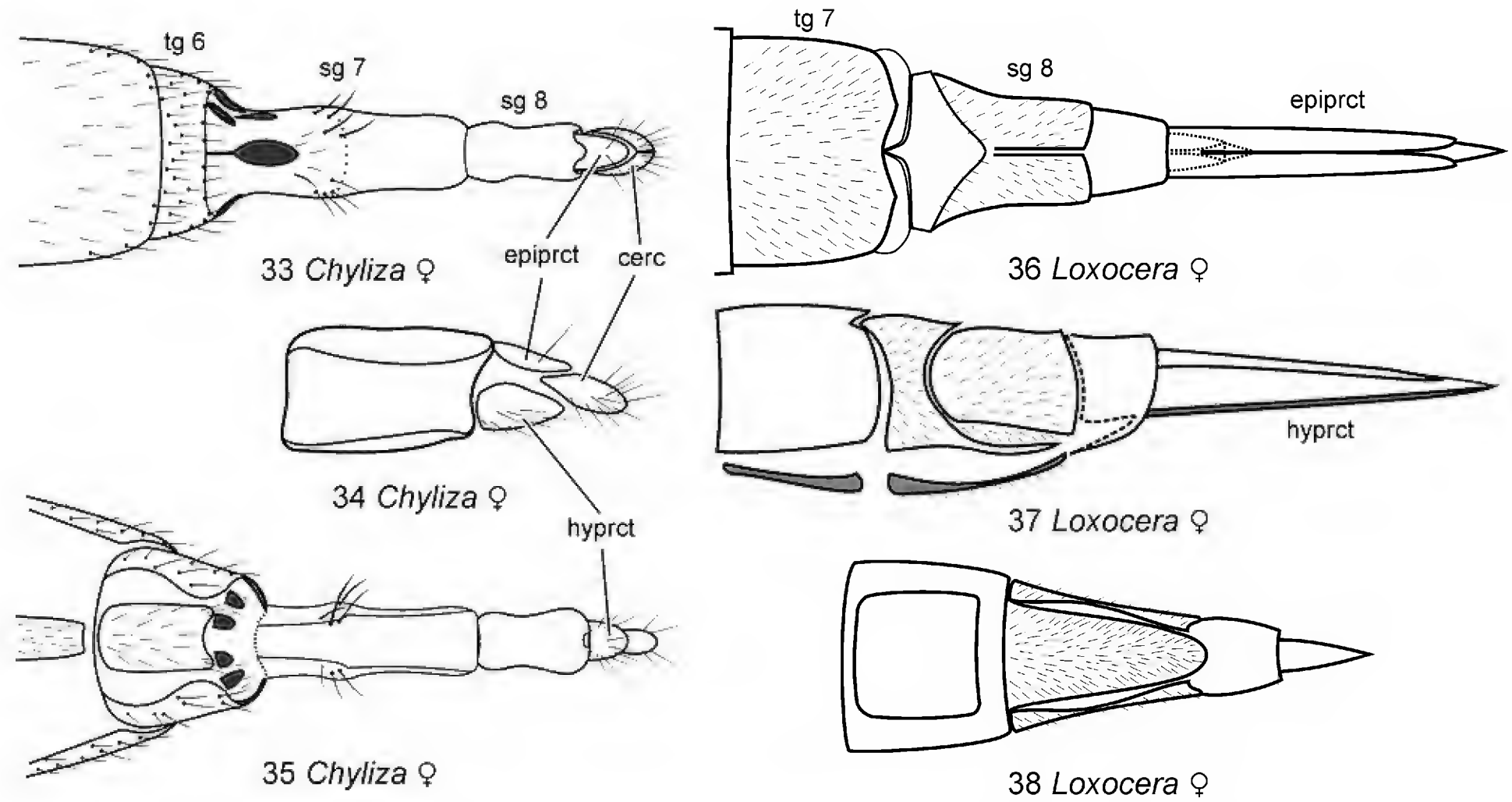
***Belobackenbardia* Shatalkin** (Belobackenbardiinae)**.** An endemic genus of three described species only known from type

material collected in South Africa. *Belobackenbardia* species occur in mountain ranges with indigenous *Podocarpus* forest, usually on low undergrowth, or possibly on low vegetation along the margins of small streams (B.R. Stuckenberg, *in litt.*). The biology and immature stages remain unknown and no modern identification key is currently available.

***Chamaepsila* Hendel** (Psilinae: Psilini)**.** This mainly Holarctic genus was established for species of *Psila* exhibiting short antennae and developed postocellar setae. Steyskal (1987: 782) did not recognise this taxon, regarding it as "… based mainly on weak chaetotactic characters …" and applied the name *Psila* for species in the American fauna. Buck (2010: 839) in the *Manual of Central American Diptera* followed Steyskal. Shatalkin (1989) and Iwasa (1998: 182) also followed Steyskal's concept of *Psila*, as some Asian species of *Chamaepsila* and *Psila sensu stricto* have an intermediate combination of characters. Some authors regard *Chamaepsila* as a subgenus of *Psila*, in particular Cogan (1977: 25; 1980: 590) for Oriental and Afrotropical species. European authors are inclined to treat *Chamaepsila* as a genus (Hennig 1941: 16; Soós 1984: 29; Verbeke 1952). This opinion has been supported by Evenhuis (1989: 473) and is accepted here. Psilini is divided into eight morphological groups, which are well-diagnosed (see diagnostic characters in Shatalkin & Merz 2010: 781, table 1). The genus *Chamaepsila* includes the majority of species of Psilini and is distributed throughout most zoogeographical regions, but is absent from the Neotropics and Australia (introduced in New Zealand). It is poorly represented in the Afrotropical Region and includes two endemic species, recorded from Democratic Republic of Congo, Ethiopia, Kenya, Rwanda and Uganda (Cogan 1980: 590; Shatalkin 2002) and two alien invasive species. Biology and immature stages of Afrotropical species are known for the two invasive species. No modern identification key to species is currently available.

***Chyliza* Fallén** (Chylizinae)**.** A large genus of 118 described species occurring in all zoogeographical regions, except Antarctica. The Afrotropical fauna comprises 27 described species, recorded from Burundi, Democratic Republic of Congo and Rwanda (Cogan 1980: 590). Verbeke (1952) proposed the subgenus *Ctenochyliza* for the two Afrotropical species with yellow palpi (*Ch. overlaeti* Verbeke, 1952 and *Ch. leae* Verbeke, 1952). Verbeke did not designate a type species for *Ctenochyliza*, hence that name is unavailable (Cogan 1980: 590). Major publications dealing with Afrotropical *Chyliza* include those of Verbeke (1952, 1963, 1968) and Lindner (1956). Prior to these works, only one species of *Chyliza* was recorded (Loew 1874). Biology and immature stages of Afrotropical species remain unknown. Sixteen species were keyed by Verbeke (1952).

***Loxocera* Meigen** (Psilinae: Loxocerini)**.** A heterogeneous genus of 55 described species occurring in all zoogeographical regions, except Antarctica. The 14 known Afrotropical species, described by Bezzi (1908), Hennig (1940), Loew (1874), Speiser (1910) and Verbeke (1952, 1956, 1963, 1968), have a continental Afrotropical distribution. They form a monophyletic group of generic or subgeneric rank with similarities to *Loxocerosoma* and *Imantimyia*. Characters of the male terminalia,

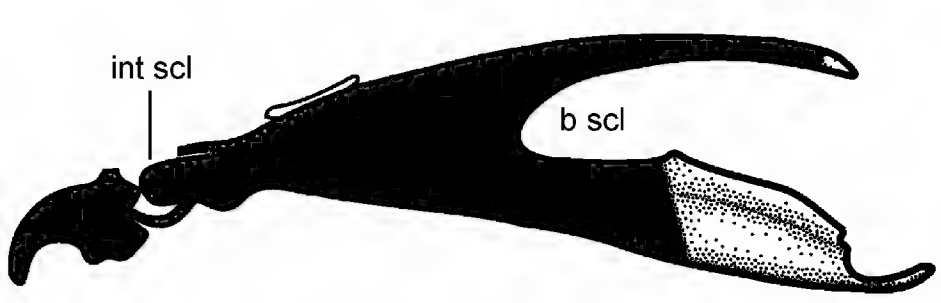


Figs 65.33–38. Female terminalia of Psilidae: (33) *Chyliza rwindiensis* Verbeke, dorsal view; (34) same, lateral view; (35) same, ventral view; (36) *Loxocera macrogramma* Speiser, dorsal view; (37) same, lateral view; (38) same, ventral view.

Abbreviations: cerc – cercus; epiprct – epiproct; hyprct – hypoproct; sg – segment; tg – tergite.

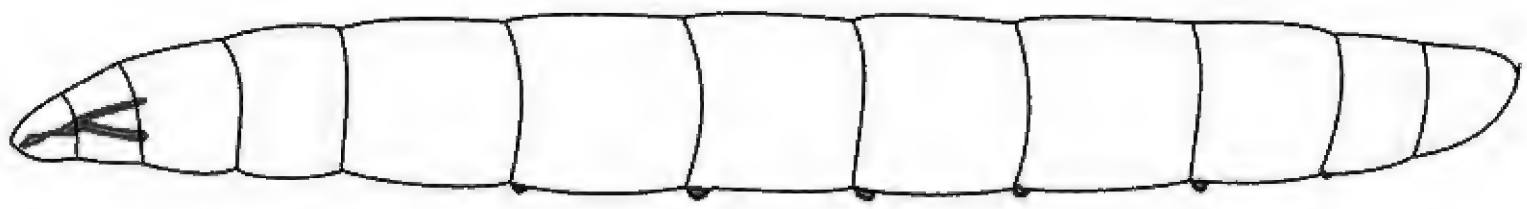
particularly the structure of epandrium (Fig. 19), indicate that Afrotropical *Loxocera* differ, not only from *Loxocerosoma* and *Imantimyia*, but also from Palaearctic and Oriental *Loxocera* species. Biology and immature stages of Afrotropical species remain unknown. Four species were keyed by Speiser (1910: 193) and eleven species by Verbeke (1963).

***Loxocerosoma* Verbeke** (Psilinae: Loxocerini)**.** An endemic Afrotropical genus with three described species and at least two undescribed species known from Madagascar. The type species, *L. psiloides* Verbeke, 1968, is recorded from Democratic Republic of Congo and two species, *L. glabra* (Verbeke, 1956) and *L. seyrigi* (Verbeke, 1956), from Madagascar. Buck & Marshall (2006*b*: 218) mentioned that "… *Loxocerosoma* was separated from *Loxocera* on very tenuous grounds". Malagasy species exhibit more clear distinctions in chaetotaxy and especially in the structure of the male terminalia. This questions the generic identity of *L. psiloides* and the Malagasy species and requires corroboration by examination of the male terminalia of the type species. Biology and immature stages remain unknown. Two Malagasy species were included in the identification key to *Loxocera* by Verbeke (1963).

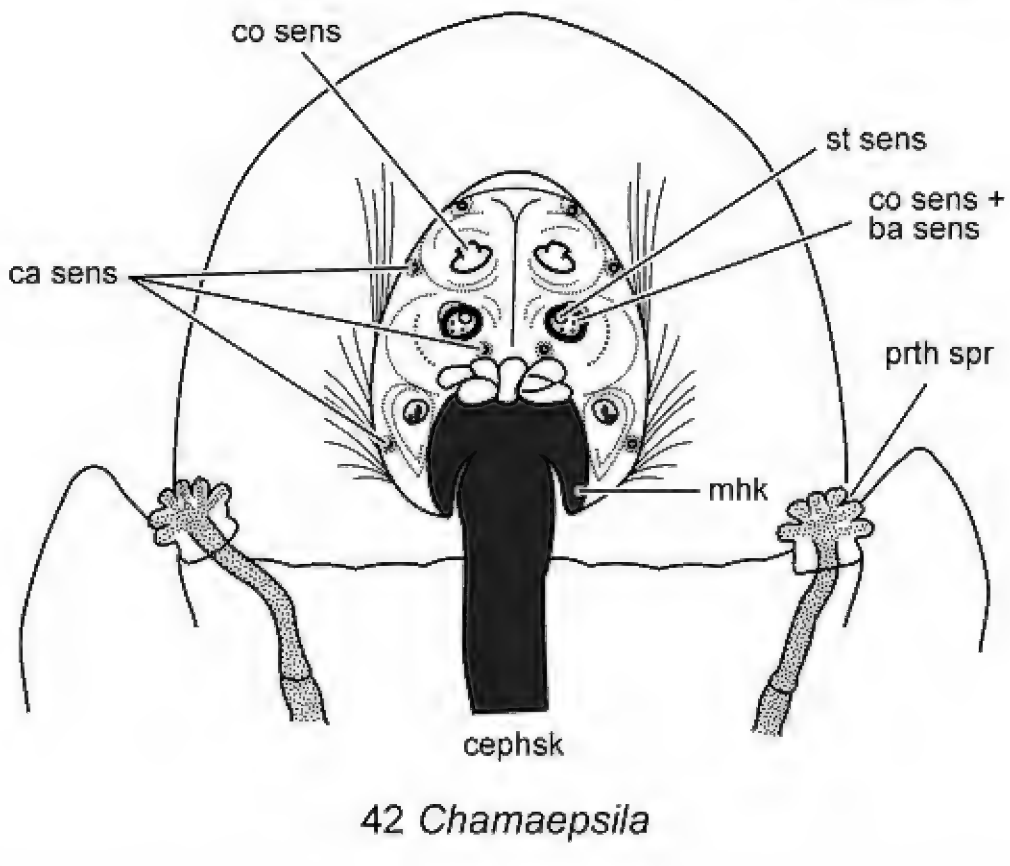


39 *Chamaepsila*

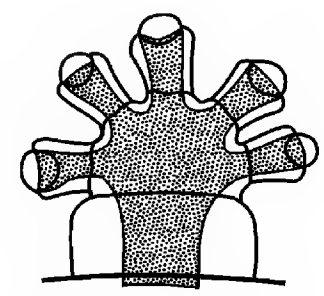
40 *Chamaepsila*



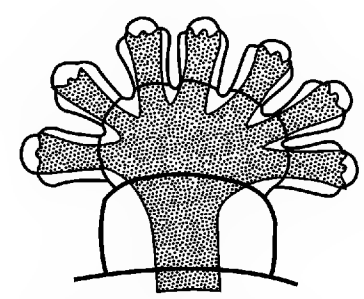
41 *Chamaepsila*



42 *Chamaepsila*



43 *Chamaepsila*



44 *Chamaepsila*

Figs 65.39–44. Immature stages of Psilidae: (39) cephaloskeleton of *Chamaepsila rosae* (F.), lateral view (non-Afrotropical); (40) same, posterior spiracles, caudal view; (41) same, third-instar larva, lateral view; (42) same, distribution of sensillae on cephalic lobes of dissected pseudocephalon, anterior view; (43) same, prothoracic spiracle, dorsal view; (44) prothoracic spiracle of *C. nigricornis* (Meigen), dorsal view (non-Afrotropical). Figs 39, 40 (after Hennig 1941, figs 13, 14c), Fig. 41 (after Smith 1989, fig. 364), Fig. 42 (after Ryan & Behan 1973, fig. 1), Figs 43, 44 (after Osborne 1961, figs 15, 16).

Abbreviations: b scl – basal sclerite; ba sens – basiconic sensillum; ca sens – campaniform sensillum; cephsk – cephaloskeleton; co sens – coeloconic sensillum; int scl – intermediate sclerite; mhk – mouthhook; prth spr – prothoracic spiracle; st sens – styloconic sensillum.

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CONOPIDAE 66

(Thick-headed Flies)

Jens-Hermann Stuke

Fig. 66.1. Female of *Stylogaster* sp. (South Africa) (photograph © S.A. Marshall).

Diagnosis

Small- to large-sized acalyptrate flies (3–25 mm), some species brightly coloured, often with metallic shiny pattern on thorax and abdomen (Figs 2–32); head large, usually broader than thorax (Figs 33–39); wing (Figs 63–66) and legs (Figs 1–32) moderately long; wing may have obvious pattern; many Conopinae exhibit striking mimicry of aculeate Hymenoptera.

Head with antenna 3-articled; arista with 1–3 articles (Figs 54–58); in Conopinae arista stylus-like, inserted apically on postpedicel and pedicel usually elongate (Figs 57, 58); antennae in other subfamilies more typical of acalyptrate flies (Figs 55, 56); compound eyes widely separated (Figs 40–53), without sexual dimorphism, without ommatrichia and lacking obvious colouration (Figs 33–39); some *Stylogaster* Macquart (the sole genus of Stylogastrinae), with obviously enlarged anteriomedian ommatidia facets (Figs 1, 38); ocelli reduced or absent in most Conopinae, 2–3 ocelli in other Conopidae; only Conopinae with distinct vertex (Figs 40–46), Dalmanniinae, Myopinae, Stylogastrinae and Zodioninae with ocellar triangle that may cover most of frons and may be homologous with vertex of Conopinae (Figs 47, 51, 53); ptilinal fissure distinct to barely discernible (e.g., *Stylogaster*); lunule indistinct in several genera; facial grooves distinct (except in *Stylogaster* and *Tropidomyia* Williston); occiput usually markedly inflated; proboscis usually distinctly longer than head (e.g., Figs 13, 22) (short in *Leopoldius* Rondani, Fig. 16); Dalmanniinae, Myopinae and Stylogastrinae with elongate labellum, *ca* as long as prementum and connected to prementum by moveable joint (Figs 60, 62), Conopinae and Zodioninae with short labellum without moveable joint (Fig. 59); palpus 1-segmented, or in

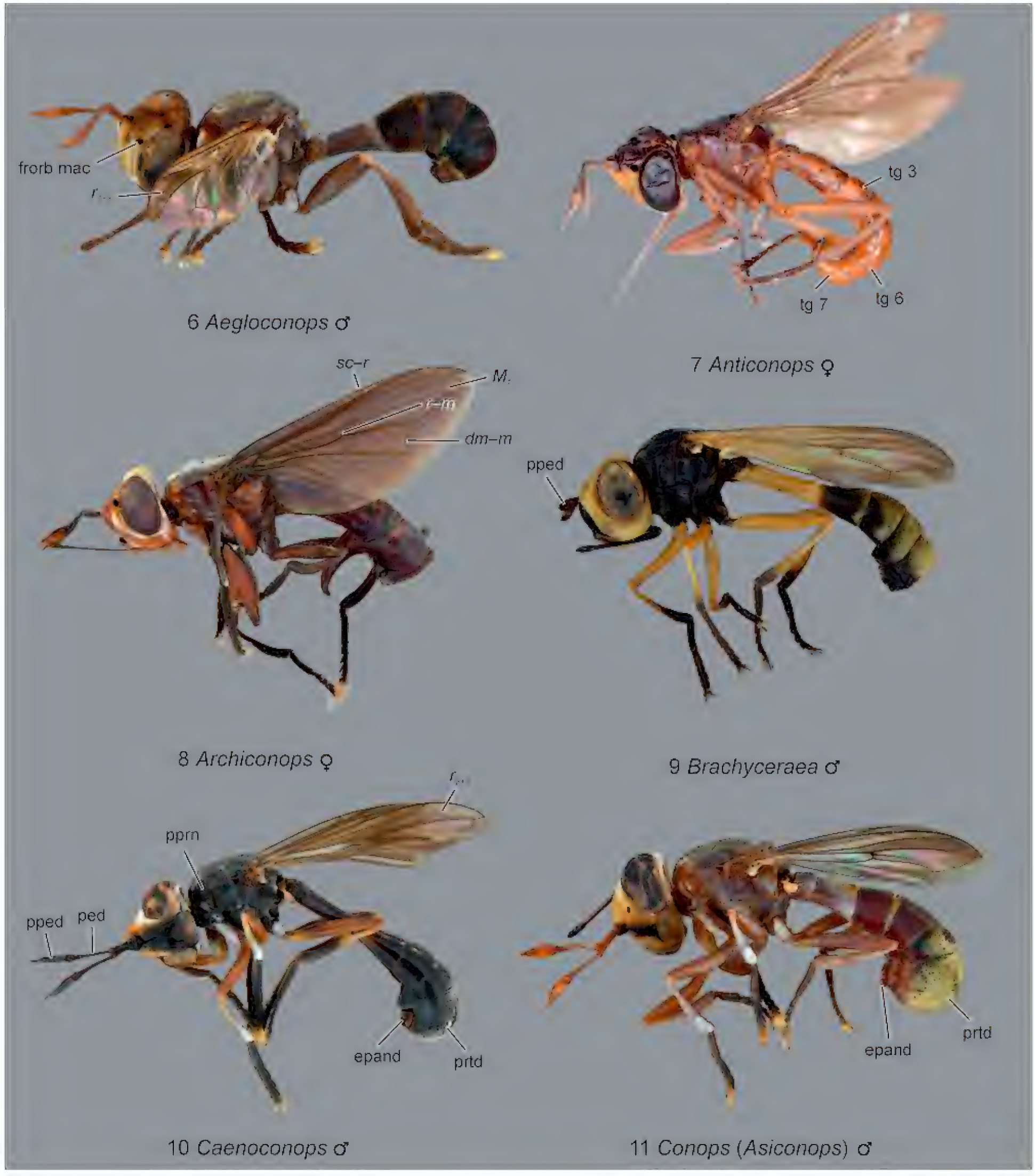
Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2021. Manual of Afrotropical Diptera. Volume 3. Brachycera—Cyclorrhapha, excluding Calyptratae. *Suricata* 8. South African National Biodiversity Institute, Pretoria; pp. 1557–1586.

some Conopinae and Stylogastrinae, reduced or entirely absent; head and thoracic setation almost entirely reduced in Conopinae, more or less reduced or difficult to discern amongst long, strong setulae in Dalmanniinae, Myopinae and Zodioninae, typical acalyptrate setation only apparent in *Stylogaster* and fossil genera; at most 1–2 ocellar setae, 1 postocellar seta, 1 medial and 1 lateral vertical seta, 0–7 fronto-orbital setae and several setae which may be homologous with frontal setae; without vibrissa.

Thorax subquadrate, with short to long setulae on scutum and variable quantity of setulae on scutellum and/or pleura; presence of setae difficult to ascertain in non-stylogasterine genera, due to presence of several strong setae or setulae which cannot be differentiated and number may vary intraspecifically; in *Stylogaster* 2 notopleural setae, up to 2 supraalar setae, 1–2 postalar setae, 1 prescutellar dorsocentral seta, 1–2 scutellar setae, 1 anepimeral seta and 1 propleural seta above fore coxa. Wing (Figs 63–66) with costal vein (*C*) and subcostal vein (*Sc*) without breaks; subcostal–radial crossvein (*sc–r*) only developed in Conopinae and Zodioninae; vein R_1 without setulae; basal radial cell (*br*) elongate, distinctly longer than basal medial cell (*bm*); veins R_{4+5} and M_1 strongly convergent towards wing margin; cell r_{4+5} open, or closed apically in some Conopinae and Zodioninae, vein $R_{4+5}+M_1$ distinct in Conopinae only (Fig. 63); vein *CuA+CuP* reaching or almost reaching wing margin; vein A_1 not reaching wing margin; anterior cubital cell (*cua*) closed, distinctly longer than cell *bm* in Conopinae, Myopinae and Zodioninae, short in Dalmanniinae and Stylogastrinae (Fig. 65); basal medial crossvein (*bm–m*) only complete in Stylogastrinae (Fig. 65); false vein most obvious in cell r_{4+5}, but other more or less distinct folds may be apparent in cell r_{2+3}, discal medial cell (*dm*), fourth medial cell (m_4) and cell *cua* (Figs 63, 64); Stylogastrinae without distinct false veins (Fig. 65). Legs moderately long (Figs 1–32), covered with setulae, sometimes spines, usually without distinct colour patterns, although may exhibit rings or maculae; posterior surfaces of fore and mid tibiae with obvious silver dusted fields distally in several genera; preapical dorsal setae on tibiae apparent only in Myopinae, Zodioninae and indistinctly in Dalmanniinae; mid coxal prong absent; fore tibia with distinct, dense black to brown setulae areas ventrally at tip and ventrally and posteriorly at tip of hind tibia.

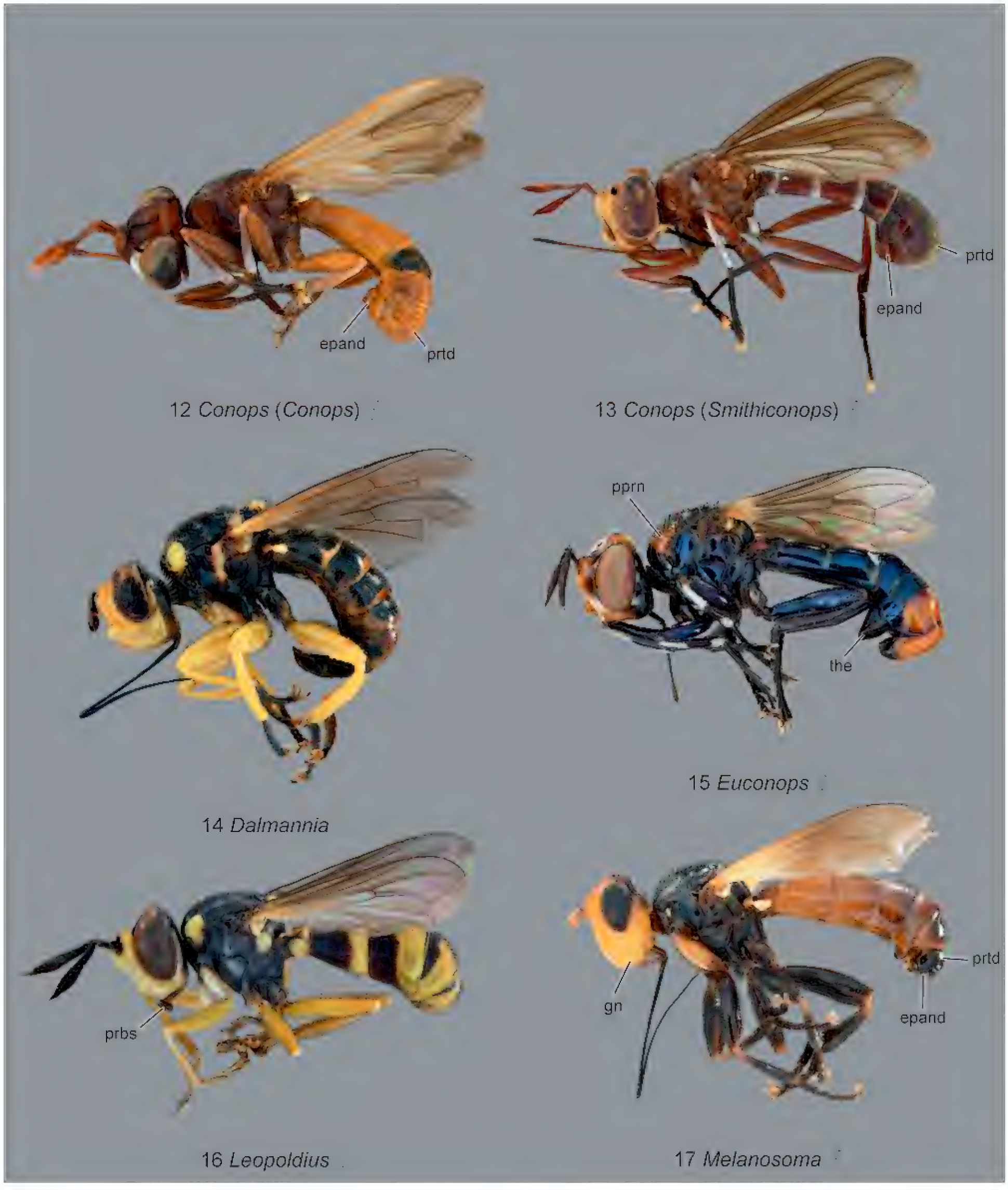
Male abdomen with 5 unmodified segments (Fig. 71), may be constricted at base with segment 3 broader posteriorly; tergites 1 and 2 more or less fused; tergite and sternite 5 fused in some Conopinae; male terminalia (postabdomen)

Figs 66.2–5. Photographs of living Afrotropical Conopidae: (2) *Archiconops pseudoerythrocephalus* Stuke ♀ (Zambia); (3) *Conops aurantius* Brunetti ♀ (Zambia); (4) *Paramyopa oestracea* (Loew) ♂ (South Africa); (5) *Thecophora* sp. ♂ (South Africa). Figs 2, 3 (photographs © W. van Niekerk), Fig. 4 (photograph © A. Sander), Fig. 5 (photograph © P. Herbst).



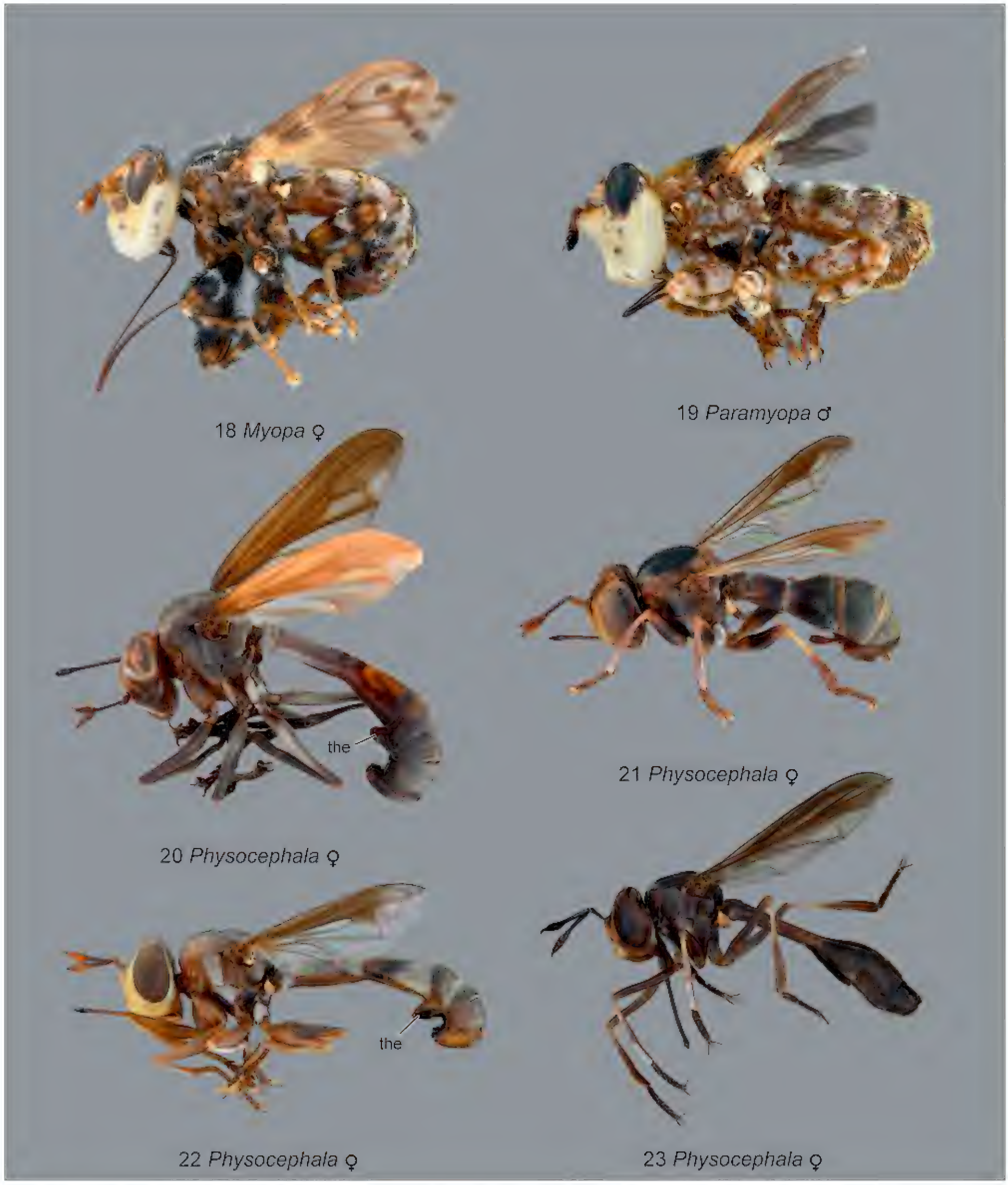
Figs 66.6–11. Habitus of Conopidae (lateral views): (6) *Aegloconops quadripunctatus* (Kröber) ♂; (7) *Anticonops abdominalis* Kröber ♀; (8) *Archiconops crypticus* Stuke ♀; (9) *Brachyceraea brevicornis* (Loew) ♂ (non-Afrotropical); (10) *Caenoconops bicolor* (Kröber) ♂; (11) *Conops* (*Asiconops*) *ferrugineus* Kröber ♂.

Abbreviations: *dm–m* – discal medial crossvein; epand – epandrium; frorb mac – fronto-orbital macula; M_1 – first branch of media; ped – pedicel; pped – postpedicel; pprn – postpronotum; prtd – protandrium; r_{2+3} – second + third radial cell; *r–m* – radial–medial crossvein; *sc–r* – subcostal–radial crossvein; tg – tergite.



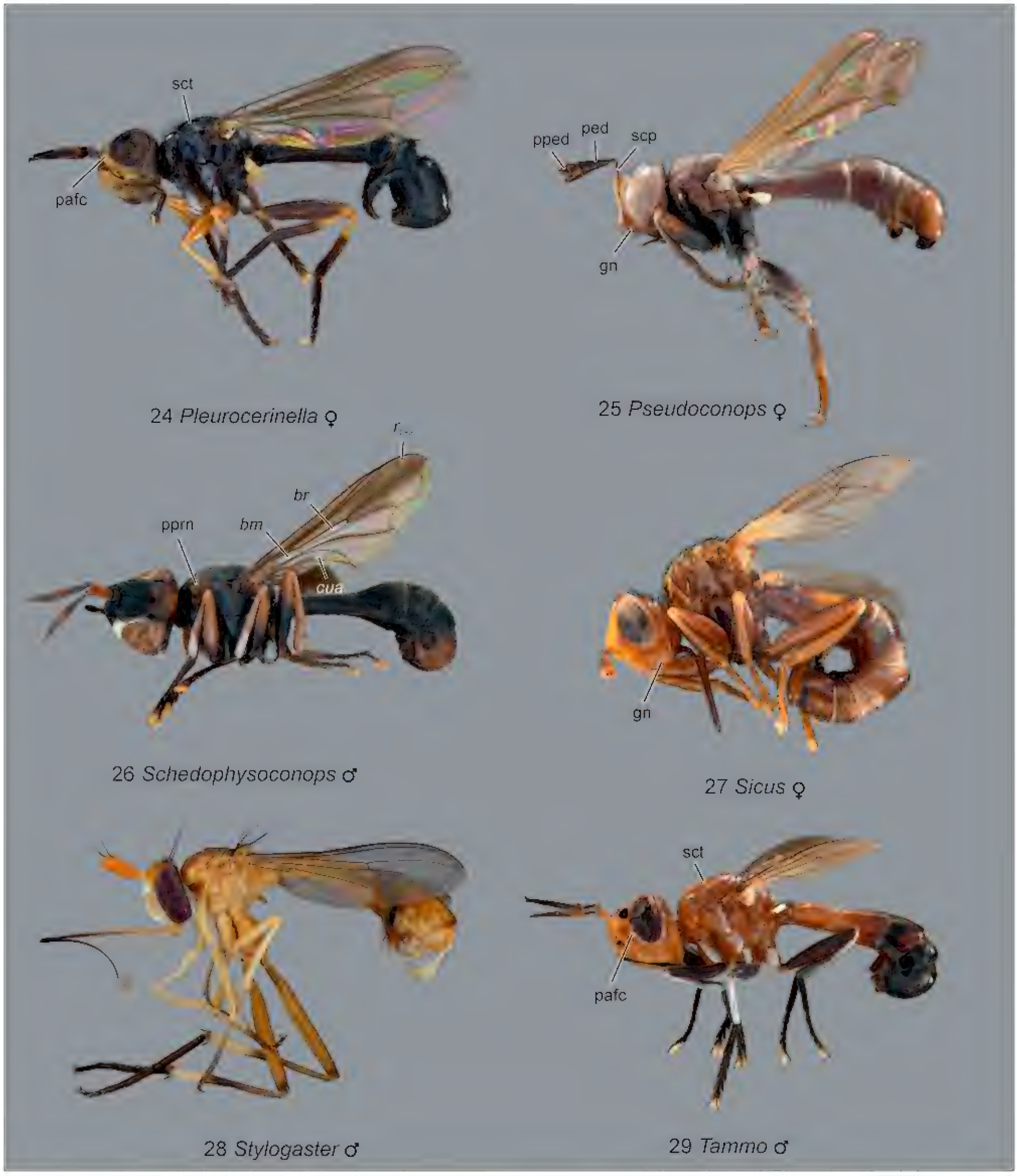
Figs 66.12–17. Habitus of Conopidae (lateral views): (12) *Conops* (*Conops*) *aurantius* Brunetti ♂; (13) *C.* (*Smithiconops*) *rondanii* Bezzi ♂; (14) *Dalmannia aculeata* (L.) ♀ (non-Afrotropical); (15) *Euconops bellus* Kröber ♀; (16) *Leopoldius coronatus* (Rondani) ♀ (non-Afrotropical); (17) *Melanosoma bicolor* (Meigen) ♂ (non-Afrotropical).

Abbreviations: epand – epandrium; gn – gena; pprn – postpronotum; prbs – proboscis; prtd – protandrium; the – theca.



Figs 66.18–23. Habitus of Conopidae (lateral views): (18) *Myopa picta* Panzer ♀ (non-Afrotropical); (19) *Paramyopa oestracea* (Loew) ♂; (20) *Physocephala bimarginipennis* Karsch ♀; (21) *P. abdominalis* (Kröber) ♀; (22) *P. antiqua* (Wiedemann) ♀; (23) *P. spinipes* (Camras) ♀.

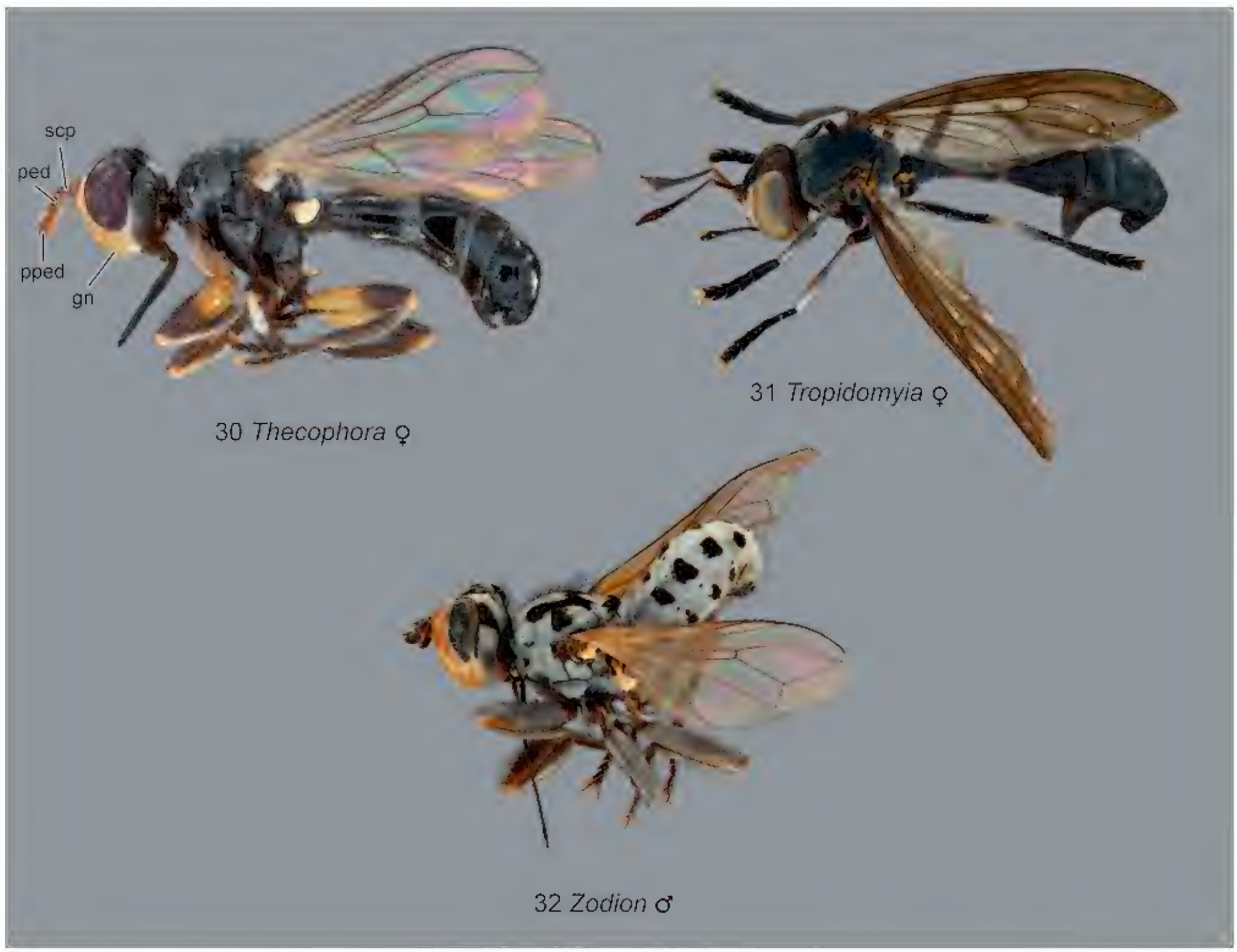
Abbreviation: the – theca.



Figs 66.24–29. Habitus of Conopidae (lateral views): (24) *Pleurocerinella kirkspriggsi* Stuke ♀; (25) *Pseudoconops antennatus* Camras ♀; (26) *Schedophysoconops longicornis* (Kröber) ♂; (27) *Sicus ferrugineus* (L.) ♀ (non-Afrotropical); (28) *Stylogaster kirkspriggsi* Stuke ♂; (29) *Tammo rufus* (Camras) ♂.

Abbreviations: *bm* – basal medial cell; *br* – basal radial cell; *cua* – anterior cubital cell; gn – gena; pafc – parafacial; ped – pedicel; pped – postpedicel; pprn – postpronotum; r_{2+3} – second + third radial cell; scp – scape; sct – scutum.

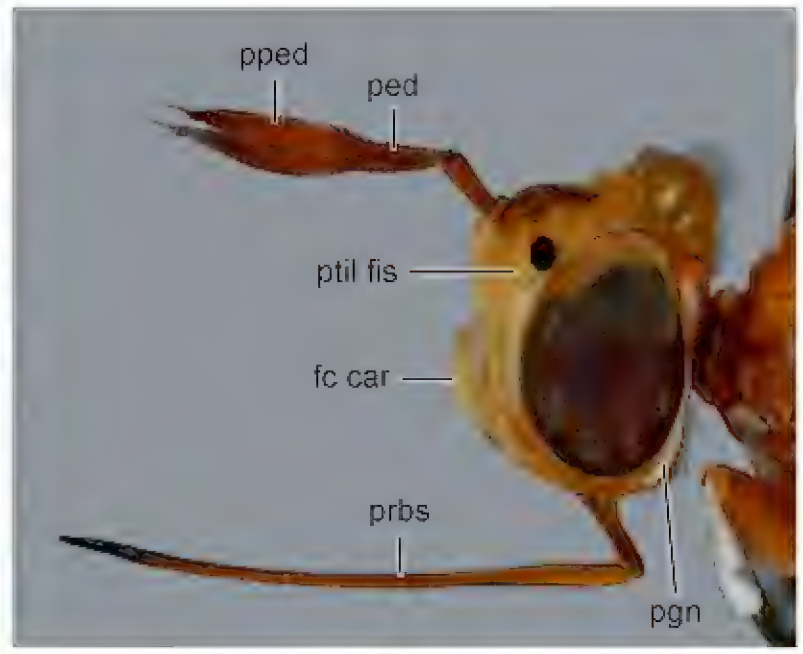
with well-developed epandrium and cercus; surstyli usually reduced or vestigial in Conopinae, Dalmanniinae and Myopinae; hypandrium well-developed, more or less uniform in Conopinae, Dalmanniinae, Myopinae and Zodioninae (e.g., Figs 83, 85); hypandrial sheath anteriorly directed, may surround phallus entirely; postgonite inconspicuous (may terminate in membranous postgonite evagination); postgonite evagination often with microtrichia or sclerotisations; 2 strong, posteriorly directed lateral hypandrial bars in all genera, except *Dalmannia* Robineau-Desvoidy and *Zodion* Latreille; distiphallus may bear taxonomically important structures, such as microtrichia, setulae, setae, spicules, sclerotised plates or lateral evaginations and may be greatly elongated (as in *Dalmannia*); spermathecal duct and sperm pump membranous; ejaculatory apodeme small and weakly sclerotised; male terminalia conspicuously different in *Stylogaster* (Figs 76, 77), with cercus longer than epandrium (Fig. 78); surstylus well-developed and species-specific; hypandrial sheath strikingly projected anteriorly, without hypandrial arms or bars; basiphallus clearly discernible, *ca* as long as hypandrium; distiphallus small; at least some species with conspicuous anteriorly directed hemispherical extension of hypandrium surrounding phallus ventrally; spermathecal duct and pump weakly to distinctly sclerotised; sperm pump conspicuous, large; female preabdomen 6-segmented (Fig. 72); sternites 1 and 2 more or less fused; tergite and sternite 5 fused in Conopinae; tergite and sternite 6 fused in Stylogastrinae; sternite 5 usually enlarged in Conopinae, Myopinae and Zodioninae, forming ventrally protruding "theca", with obvious field(s) of setulae on posterior surface (Fig. 87); tergite 7 distinctly bent ventrally; tergite 8 laterally with strong tooth on either side, associated with ventral sclerotisation (Fig. 86); sternite 8 conspicuous, with thick black setae and long setulae; segment 8 forming conspicuous protruding spatulate structure in some Afrotropical *Physocephala* Schiner (Figs 88, 89); *Dalmannia* with strikingly different ovipositor structure at tip of abdomen; *Stylogaster* with third form of



Figs 66.30–32. Habitus of Conopidae (lateral views): (30) *Thecophora pilosa* (Kröber) ♀; (31) *Tropidomyia ornata* Kröber ♀; (32) *Zodion perbellum* Speiser ♂.

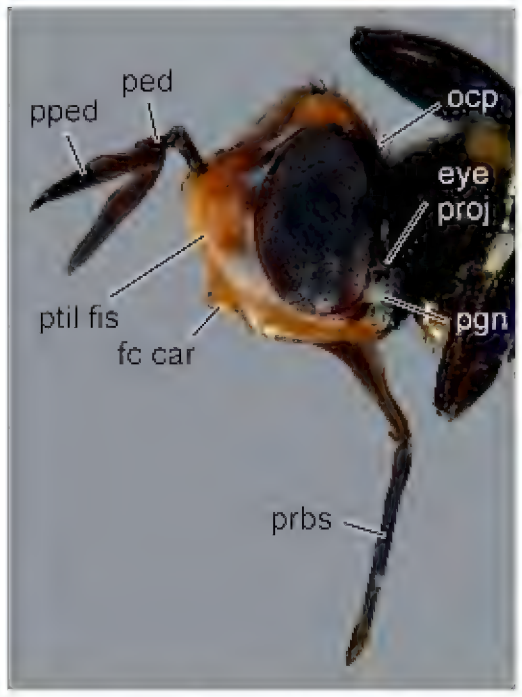
Abbreviations: gn – gena; ped – pedicel; pped – postpedicel; scp – scape.

33 *Brachyceraea* ♂

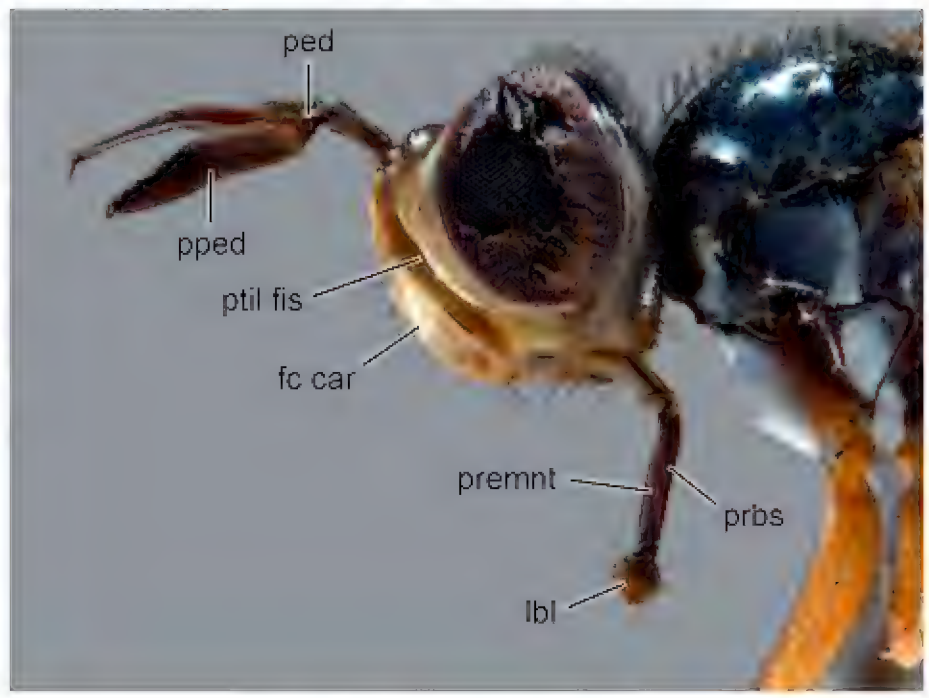


34 *Conops* (*Smithiconops*) ♀

35 *Paramyopa* ♂



36 *Euconops* ♂



37 *Pleurocerinella* ♀

38 *Stylogaster* ♂

39 *Tropidomyia* ♂

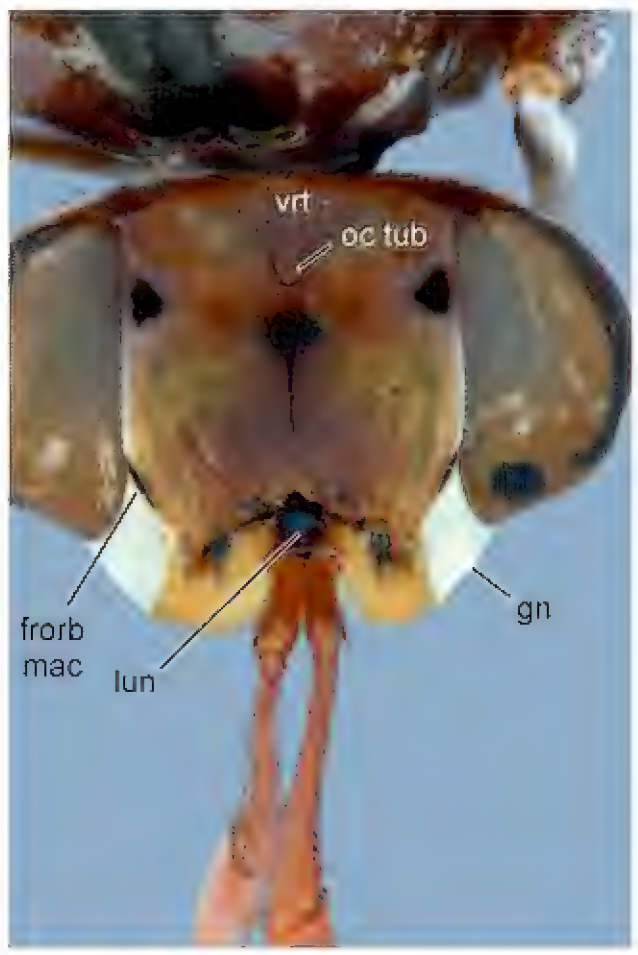
Figs 66.33–39. Heads of Conopidae (lateral views): (33) *Brachyceraea brevicornis* (Loew) ♂ (non-Afrotropical); (34) *Conops* (*Smithiconops*) *rondanii* Bezzi ♀; (35) *Paramyopa oestracea* (Loew) ♂; (36) *Euconops bellus* Kröber ♂; (37) *Pleurocerinella kirkspriggsi* Stuke ♀; (38) *Stylogaster kirkspriggsi* Stuke ♂; (39) *Tropidomyia ornata* Kröber ♂.

Abbreviations: eye proj – eye projection; fc car – facial carina; gn – gena; lbl – labellum; ocp – occiput; ped – pedicel; pgn – postgena; pped – postpedicel; prbs – proboscis; premnt – prementum; ptil fis – ptilinal fissure.

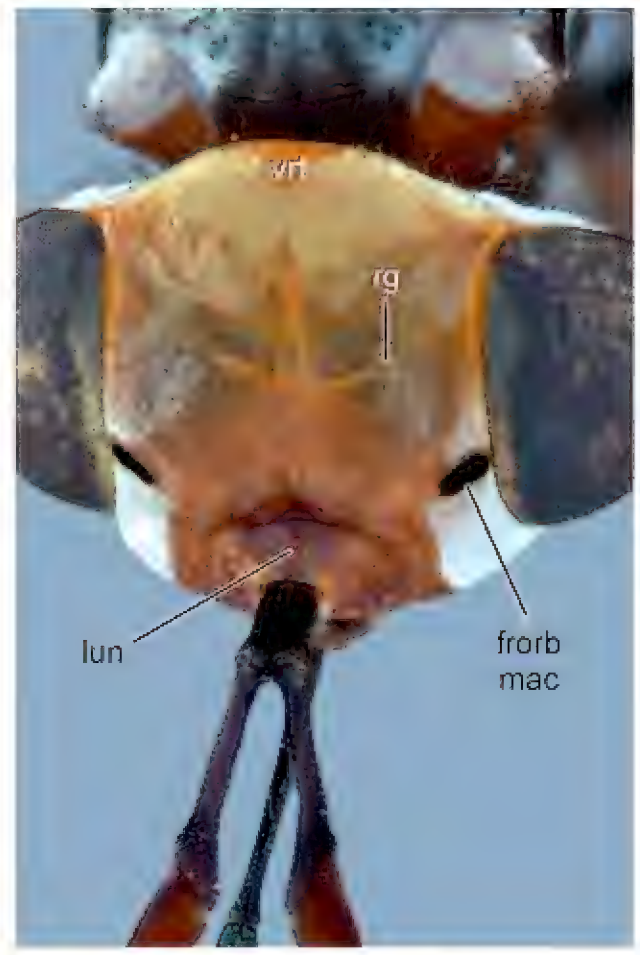
female terminalia (Figs 90, 91), with tergite 7 fused with sternite 7, tergite 8 elongate and not bent, obvious cerci directed posteriorly; vagina indistinct due to lack of sclerotisation, large sack-like ventral evagination of vagina in Conopinae, Myopinae and Zodioninae with 1 or sometimes 2 annular sclerotisations; 2 pairs of spermathecae present, but *Dalmannia* and *Stylogaster* with 2 single spermathecae only; spermathecal ducts of paired spermathecae fused shortly after leaving spermathecae, sclerotised in *Stylogaster* only.

Egg (Figs 92–98) whitish, elongated, surface smooth with chorion thin, without apparent structures; anterior end with micropyle and various appendages; egg of *Stylogaster* (Figs 92, 95) with polygonal surface network, pointed at posterior end, with distinct sclerotisation, with backwardly directed spines and membranous bladder.

Larva (Figs 99–104) white, often somewhat flattened; surface with small setae, setulae, or wart-like evaginations or tubercles;

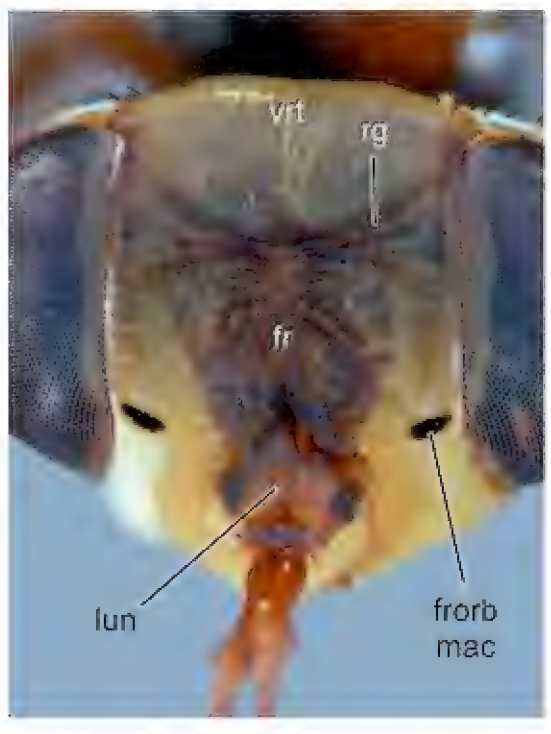


40 *Aegloconops* ♂



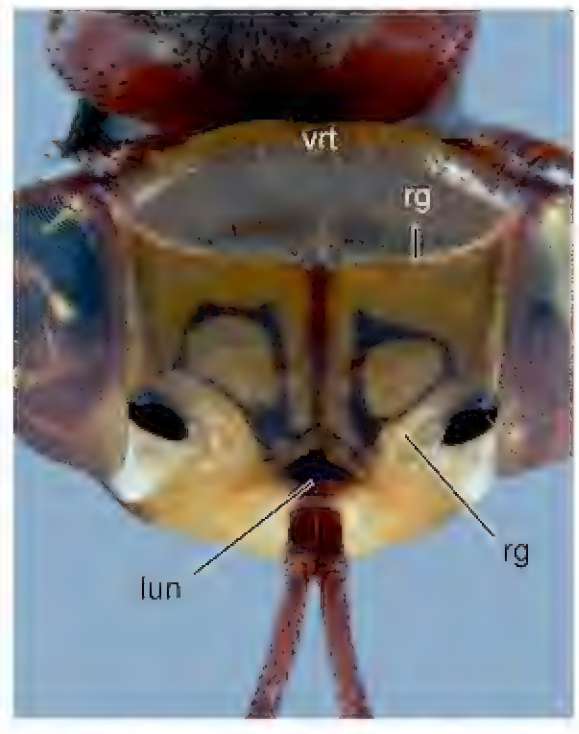
41 *Archiconops* ♀

42 *Caenoconops* ♂



43 *Conops* (*Asiconops*) ♂

44 *Conops* (*Conops*) ♂



45 *Conops* (*Smithiconops*) ♂

Figs 66.40–45. Frons of Conopidae (dorsal views): (40) *Aegloconops quadripunctatus* (Kröber) ♂; (41) *Archiconops crypticus* Stuke ♀; (42) *Caenoconops bicolor* (Kröber) ♂; (43) *Conops* (*Asiconops*) *ferrugineus* Kröber ♂; (44) *Co.* (*Co.*) *aurantius* Brunetti ♂; (45) *Co.* (*Smithiconops*) *rondanii* Bezzi ♂.

Abbreviations: fr – frons; frorb mac – fronto-orbital macula; gn – gena; lun – lunule; oc tub – ocellar tubercle; rg – ridge; vrt – vertex.

distribution of sensillae and integumental folds not described; without sclerotised structures or creeping welts for movement; pseudocephalon small, typically bearing 2 distinct antennomaxillary lobes, each with antennomaxillary complex; thoracic segments usually markedly narrow, elongated, appearing strongly attenuated in anterior part; posterior spiracles obvious, prothoracic spiracles only obvious in *Sicus* Scopoli and *Zodion*, neither prothoracic nor posterior spiracles retractile, the latter typically fused; posterior spiracular plate (Figs 100, 102, 104) strongly convex, each spiracle with variable, but with large number of spiracular openings, usually situated on tiny wart-like protuberances; without setae or spiracular gland openings on spiracles; posterior spiracles in some species with dorsal and ventral spinulose integument; cephaloskeleton with large, strongly sclerotised, entirely separated mouthhooks; labial sclerite may be present; parastomal bar usually entirely fused to basal sclerite; basal sclerite not fused dorsally, but with ventral transverse bar; basal sclerite large, with ventral and dorsal cornua; cibarium not described; larvae of *Stylogaster* quite different, with mouthhooks much smaller; thoracic segments not attenuated; posterior spiracles inconspicuous, often with conspicuous horseshoe-shaped network of trachea near surface at posterior end.

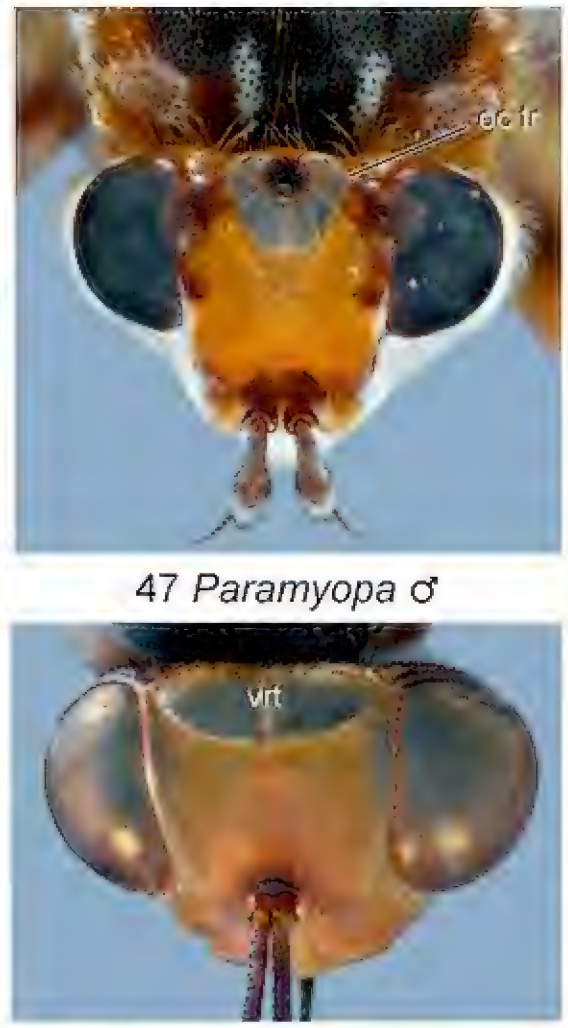
Puparium without distinctive larval shape, due to thoracic segments being retracted at pupariation; integument becoming darker with age.

Adult Conopidae are easily recognised, although the family is morphological diverse and the subfamilies quite different. Wasp-mimicking flies in other families of Diptera are regularly confused with Conopidae, however, due to their superficial similarity. This includes the genera *Ceriana* Rafinesque and *Sphiximorpha* Rondani in the Syrphidae (see Chapter 60), which are separable on wing vein M_1, which is abruptly turned up to run virtually parallel to wing margin. Some Pyrgotidae (see Chapter 72) may also be confused with Conopinae, but in such cases wing veins M_1 and R_{4+5} are parallel and not converging. Bombyliidae (see Chapter 45) of the genus *Systropus* Wiedemann are regularly confused with Conopidae, but this distinctive genus (see Chapter 45, Fig. 45.3) has an entirely different wing venation with, for example, vein R_{4+5} distinctly forked.

Biology and immature stages

Adult Conopidae feed at various flowers, but there are no species which are known to specialise on any single plant species. Nevertheless, knowledge concerning Afrotropical species is remarkably poor, with very few Afrotropical flower visiting records being available for just twelve conopid species. Stuke (2019) reported triungulin larval instars of Coleoptera: Meloidae attached to the base of the proboscis of an Afrotropical *Conops* L. species, but there are no Afrotropical records of conopid hyperparasites or predators, which have also only been reported very sparingly from other zoogeographical regions.

46 *Euconops* ♂



47 *Paramyopa* ♂

48 *Physocephala* ♀

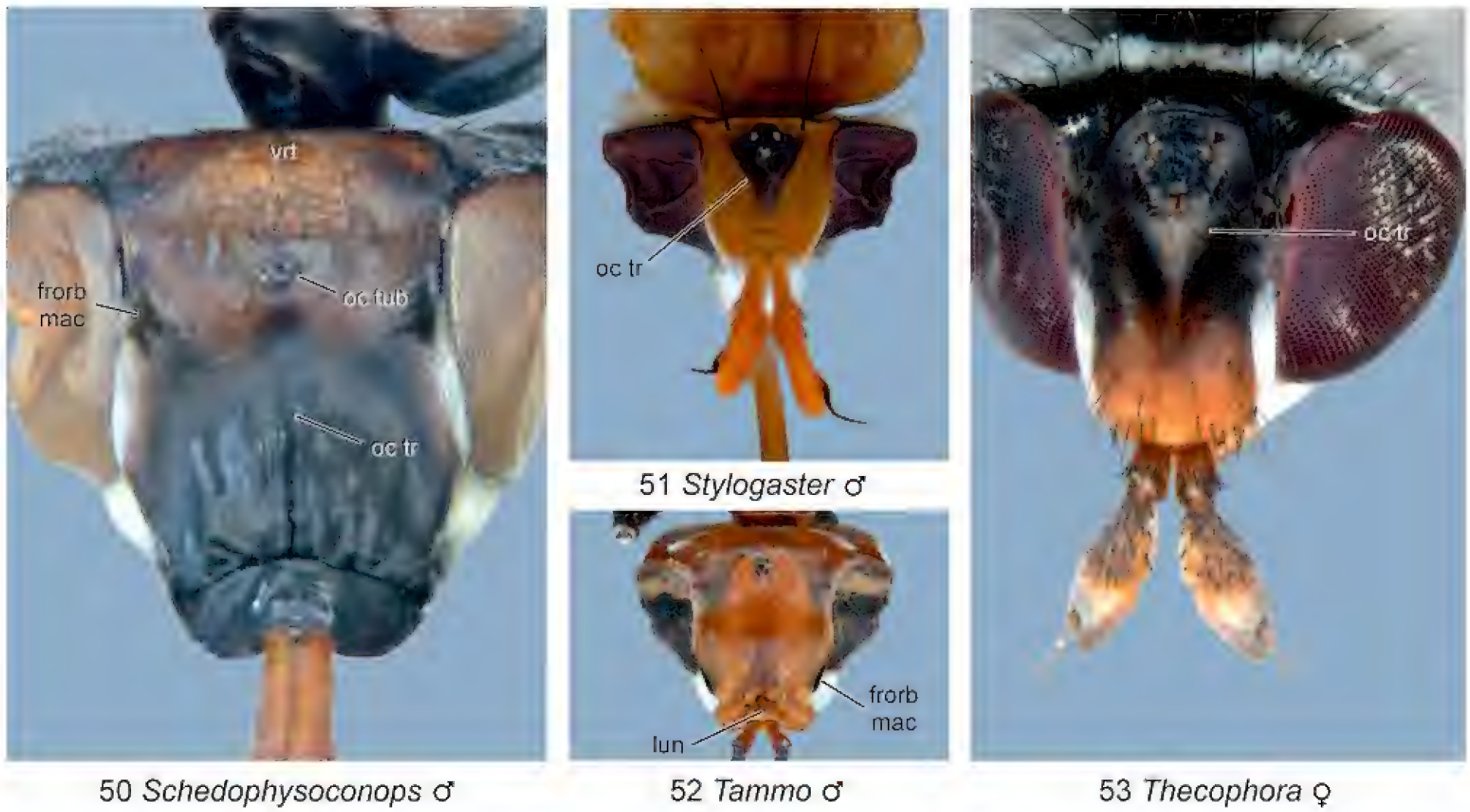
49 *Pleurocerinella* ♀

Figs 66.46–49. Frons of Conopidae (dorsal views): (46) *Euconops bellus* Kröber ♂; (47) *Paramyopa oestracea* (Loew) ♂; (48) *Physocephala antiqua* (Wiedemann) ♀; (49) *Pleurocerinella kirkspriggsi* Stuke ♀.

Abbreviations: lun – lunule; oc tr – ocellar triangle; vrt – vertex.

The larvae of Conopinae, Dalmanniinae, Myopinae and Zodioninae (Figs 99–104) are known to be endoparasitoids of Hymenoptera, mainly Aculeata. There are also some records of Conopidae reared from Orthoptera (e.g., Callot 1935; Dufour 1837), but these are considered doubtful. The few host records known from the Afrotropical Region are from *Conops* and *Physocephala* only and are listed in the "Synopsis of the fauna" section below. As far as is known from various Holarctic species, Conopidae attack their hosts at their nesting sites, or while they are visiting flowers or collecting water, *etc*. There is some discussion as to whether conopid eggs are deposited on the surface of the host or are injected into the host's body. Based on the morphology of the female abdomen, which usually bears an obvious theca and has characteristic apical spines, it is generally considered most likely that eggs are inserted into the body of the host through the intersegmental membrane (e.g., Howell 1967). Characteristic appendages on conopid eggs (Figs 96, 97) have been interpreted as structures which maintain the micropyle of the ovum exposed to the air at the exterior of the host for respiration by the embryo, until the larvae exit the egg. Gaponov (2003: 63) investigated the fine structure of the eggs of several conopid species, pointing out that a smooth surface and thin chorion is typical of parasitoid eggs that are injected into the host. Within the wider family, only the eggs of tropical *Stylogaster* species (Figs 92, 95) are known to have a (often indistinct) polygonal surface network and it is noteworthy that these are seemingly the only conopid eggs that are not almost completely implanted inside the host, but are instead injected as darts into the cuticle surface (see summary in Smith 1967). The first-instar larva may respire cutaneously, but older larvae obtain oxygen *via* the host's tracheal system (tracheae, air sacs), to which they are connected by their posterior spiracles (Figs 100, 102, 104). Conopids are not known to make a permanent connection to the host's tracheae and do not induce the formation of a respiratory funnel (Clausen 1950; Howell 1967; Keilin 1944). Usually only a single conopid larva develops within each host's abdomen. The first two larval instars feed only in the abdomen, consuming the host's hemolymph, whilst the third-instar also feeds on the other tissues of the abdomen and later also of the thorax (Howell 1967). The larva remains in the host's abdomen and reaches the thoracic tissue through the petiole, for which purpose it has only a very small pseudocephalon which is situated at the end of a narrow, extensible "trunk" formed by the anterior head segments (Figs 99, 101, 103).

Some recent studies have suggested how and why conopid larvae that develop in social Aculeata nests may alter the host's behaviour: Schmid-Hempel & Schmid-Hempel (1990) and Schmid-Hempel & Stauffer (1998) demonstrated that the foraging behaviour in *Bombus* Latreille (Apidae) is different when infested by conopids. Schmid-Hempel & Müller (1991) suggested that infested workers of *Bombus* remain outside the nest for longer periods to reduce the conopid's fitness. The host may attempt to slow down the parasitoid's development by remaining outside of the nest at night, thus exposing it



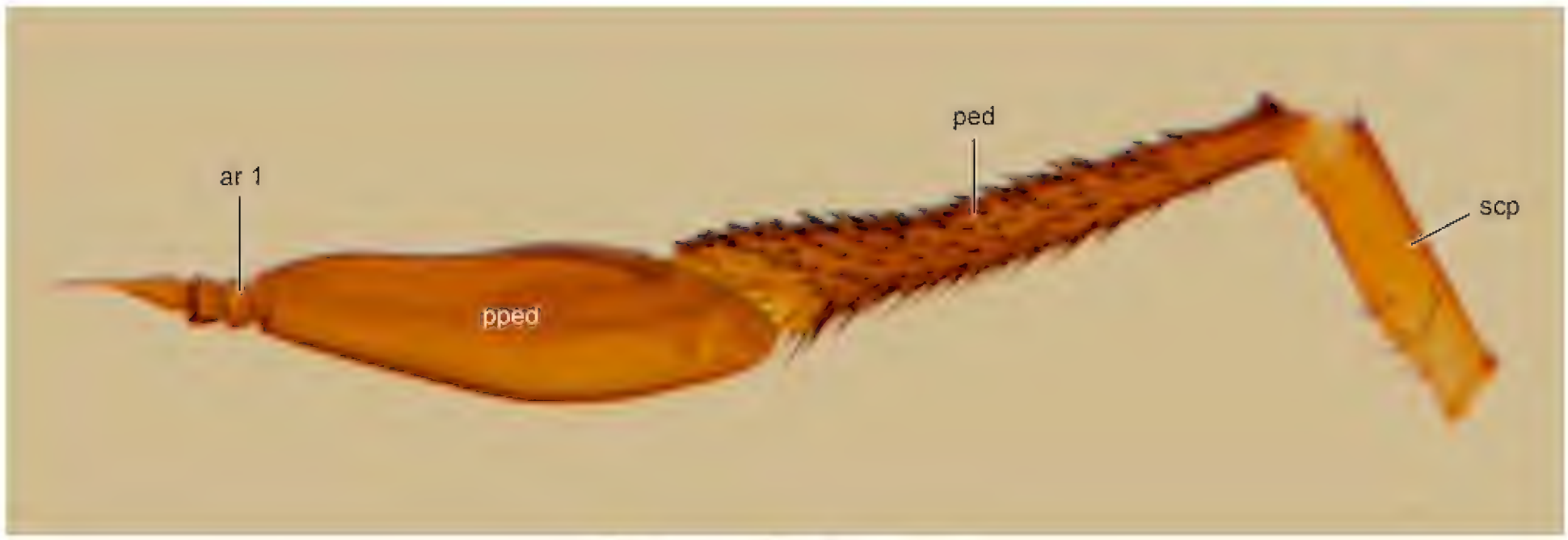
50 *Schedophysoconops* ♂ 51 *Stylogaster* ♂ 52 *Tammo* ♂ 53 *Thecophora* ♀

Figs 66.50–53. Frons of Conopidae (dorsal views): (50) *Schedophysoconops longicornis* (Kröber) ♂; (51) *Stylogaster kirkspriggsi* Stuke ♂; (52) *Tammo rufus* (Camras) ♂; (53) *Thecophora pilosa* (Kröber) ♀.

Abbreviations: frorb mac – fronto-orbital macula; lun – lunule; oc tr – ocellar triangle; oc tub – ocellar tubercle; vrt – vertex.

to reduced temperatures (Müller & Schmid-Hempel 1993). Some European *Physocephala* which attack *Bombus* stimulate fossorial behaviour, in which the host buries itself in soil before dying, potentially providing protection from scavengers and frost while overwintering (Müller 1994). The larva pupariates in the host's abdomen which is entirely filled with the conopid puparium. It is also reported that some infested hosts return to their nest before dying and that this may subsequently form the hibernation and emergence site. The adult conopid exits the host's nest while still teneral and the wings "harden" after leaving the nest. Dead host individuals of *Apis* are reported to be removed by other bees from the nest, however, and the conopids these contain presumably pupariate outside the nest.

The larval biology of Afrotropical *Stylogaster* remains a mystery. It is well-documented that adults accompany army ants of the genus *Dorylus* F. (*Anomma* Shuckard) (Formicidae), during foraging raids (Bequaert 1922; Camras 1962; Cohic 1948; Lindner 1955, 1956; Smith & Cunningham-van Someren 1985; Stuckenberg 1963). There appears to be no close relationship between *Stylogaster* and the ants, but female *Stylogaster* inject their highly modified eggs (Figs 92,



Figs 66.54–58. Antennae of Conopidae (lateral views): (54) *Conops* (*Smithiconops*) *rondanii* Bezzi; (55) *Stylogaster westwoodi* Smith; (56) *Paramyopa oestracea* (Loew); (57) *Caenoconops bicolor* (Kröber) ♂; (58) *Schedophysoconops longicornis* (Kröber) ♀.

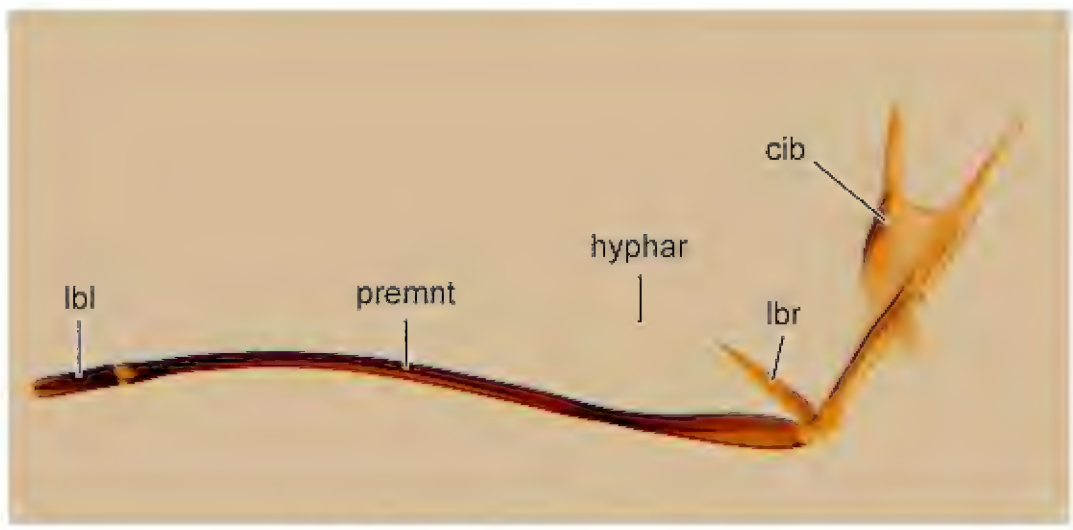
Abbreviations: ar – aristomere; ped – pedicel; pped – postpedicel; scp – scape.

95) into a range of other insects fleeing from ants. The ova of several *Stylogaster* species have been described and are readily distinguishable (Smith 1967). Many morphologically distinct *Stylogaster* ova are available in collections, but cannot be assigned to species at this time. It remains unclear whether the recorded oviposition behaviour is similar in all Afrotropical *Stylogaster*, or whether the oviposition behaviour is species-specific. Smith & Cunningham-van Someren (1985) reported three sympatric *Stylogaster* species which differ clearly in the insects on which their eggs are found: *S. varifrons* Malloch, 1930 eggs were found only on cockroach nymphs of the genus *Euloboptera* Princis and possibly *Blatella* Caudell (Blattellidae); *S. westwoodi* Smith, 1967 eggs only on the Gryllidae genera *Acanthogryllus* Saussure, *Callogryllus* Sjöstedt and *Gryllus* L. and possibly also accidentally on Araneae (Lycosidae); whilst only *S. nitens* Brunetti, 1925 eggs were found on the Diptera families Calliphoridae and Muscidae (e.g., Figs 93, 94). Jensen *et al*. (2020) found *Stylogaster* eggs among several Calliphoridae that were attracted by injured or crushed local juliform millipedes only of the genus *Tricyclea* Wulp. Jensen *et al*. (2020) pointed out that even the location on the body where *Stylogaster* eggs occur may be species-specific. Couri & Pont (2006), Jensen *et al*. (2020) and Stuke (2017) presented a recent overview of the Diptera on which *Stylogaster* eggs have been found.

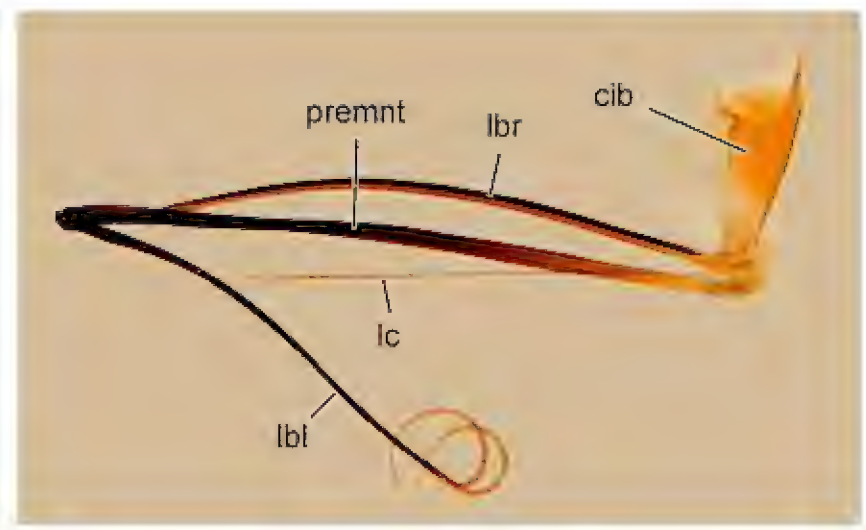
The only report of an Afrotropical *Stylogaster* larva is that of *S. cf. westwoodi* which have been found in crickets and *S. cf. varifrons* larvae found in cockroach nymphs (Smith & Cunningham-van Someren 1985). Although larvae have been sought in adult flies from which egg records have been reported, there are currently no reliable larval records (Couri & Pont 2006; Jensen *et al*. 2020). Only Berghe *et al*. (1956: 54) reported an emerged *"Stylogaster leonum"* from "… des pupes des glossines" (= pupa of *Glossina morsitans* Westwood, 1851 (Glossinidae)) and Smith (1967) identified the eclosed *Stylogaster* specimen as *S. westwoodi*. It has, therefore, been suggested that the attacked flies are only "carriers" of *Stylogaster* eggs and that these may subsequently be transferred to some other final larval host (Jensen *et al*. 2020; Stuckenberg 1963). In the Nearctic, *Stylogaster* larvae have been recorded from Gryllidae (Orthoptera) (Etzler *et al*. 2020; Woodley & Judd 1998).

Economic significance

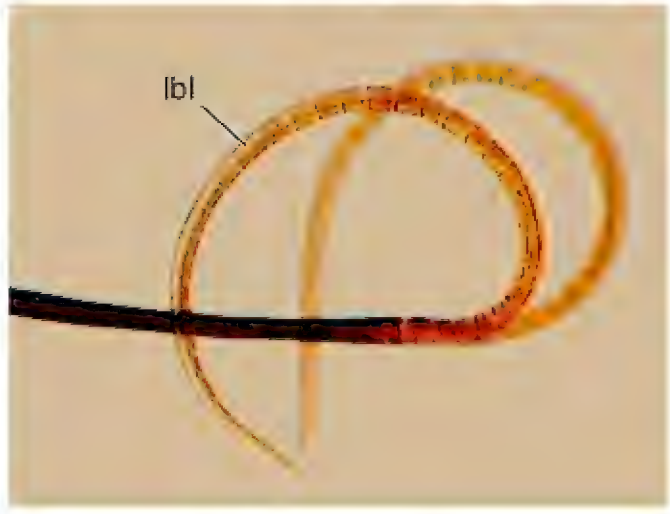
There is little information on the economic importance of Conopidae. They have been reported as parasites of *Apis* species and may cause reduced honey production (e.g., Severin 1937; Tingek *et al*. 2007). More attention has been given to



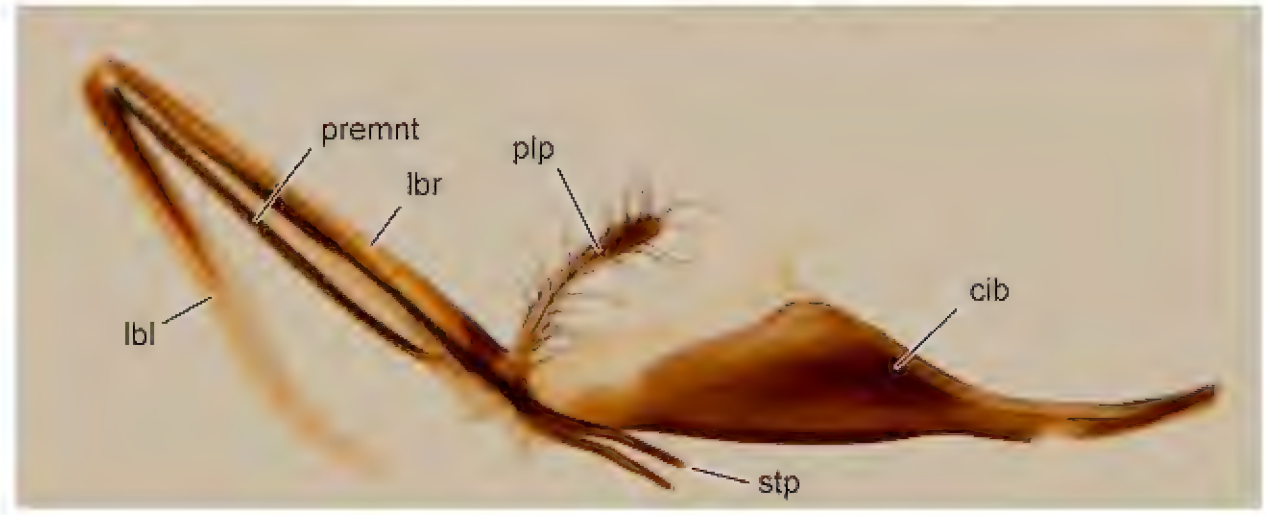
59 *Conops* (*Smithiconops*)



60 *Stylogaster*



61 *Stylogaster*



62 *Myopa*

Figs 66.59–62. Mouthparts of Conopidae (lateral views): (59) *Conops* (*Smithiconops*) *rondanii* Bezzi; (60) *Stylogaster westwoodi* Smith; (61) same, detail of labellum; (62) *Myopa buccata* (L.) (non-Afrotropical).

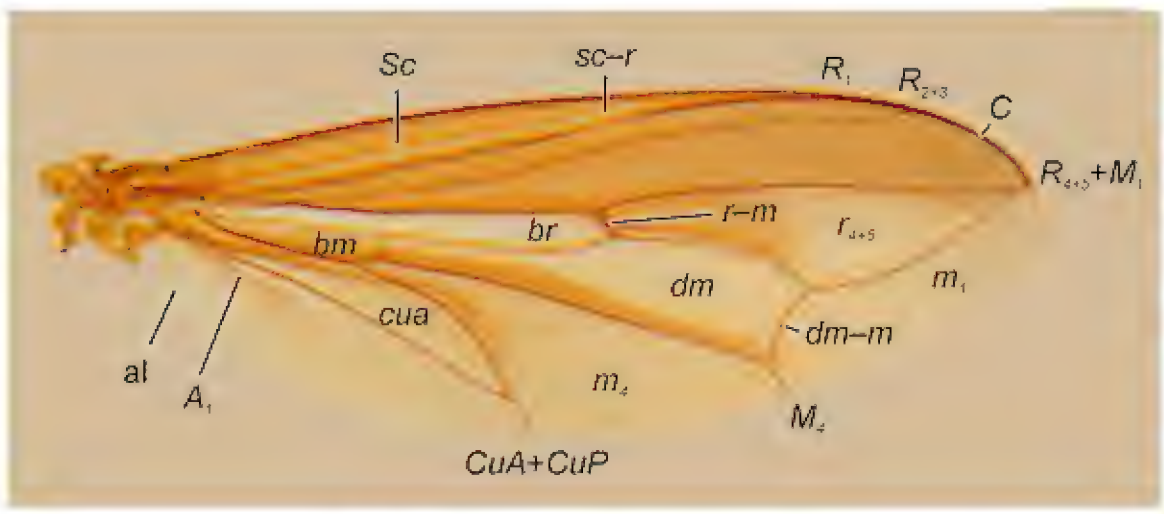
Abbreviations: cib – cibarium; hyphar – hypopharynx; lbl – labellum; lbr – labrum; lc – lacinia; plp – palpus; premnt – prementum; stp – stipes.

the high rate of parasitism of Apidae, which are important pollinators of commercial fruit, such as *Megachile rotundata* (F.) or *Nomia melanderi* (Cockerell) (e.g., Doroshina 1991; Howell 1967). No cases have come to attention which suggests there has been any serious damage to economically important bees in the Afrotropical Region. Adult Conopidae are highly likely to act as pollinators, but their significance in this regard is unknown.

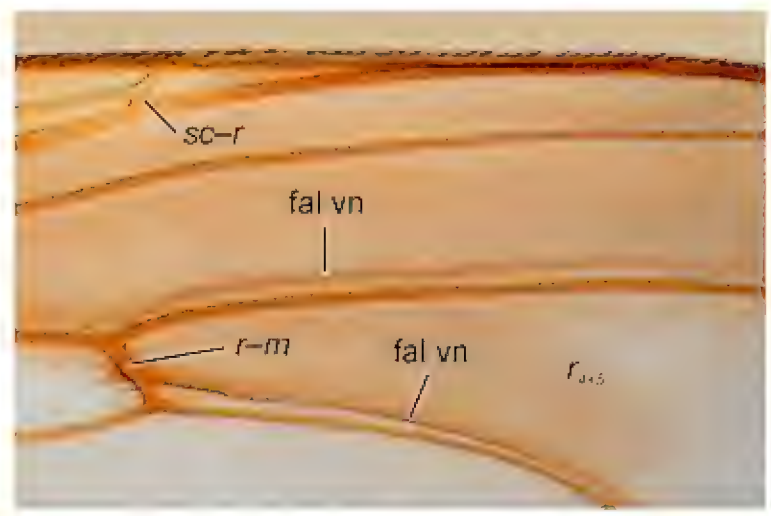
Classification

The classification of the Conopidae within the higher Diptera was discussed by Gibson *et al*. (2010). It is now widely accepted that the Conopidae belong to the Schizophora and within the Schizophora to the acalyptrate flies, but their precise position within the acalyptrate flies remains contentious. A close relationship to the Tephritoidea was postulated by Griffiths (1972: 243), Korneyev (1999: 9) and McAlpine (1989: 116), while Gibson *et al*. (2010) found Conopidae and Lauxaniidae to form a monophylum. Wiegmann & Yeates (2017: 11) and Wiegmann *et al*. (2011) placed Conopidae as sister to Sciomyzidae in the Sciomyzoidea (and Sciomyzoidea sister to Lauxanioidea). This hypothesis was adopted by Marshall (2012: 296). The analyses of Han & Ro (2005) and Han *et al*. (2002) were inconclusive, however, and depend on the cladistic method used and the DNA sequences which are taken into account. Agromyzidae, Diopsidae, Micropezidae or Pyrgotidae appear to be the closest relatives, based on their analysis of a restricted number of species and families.

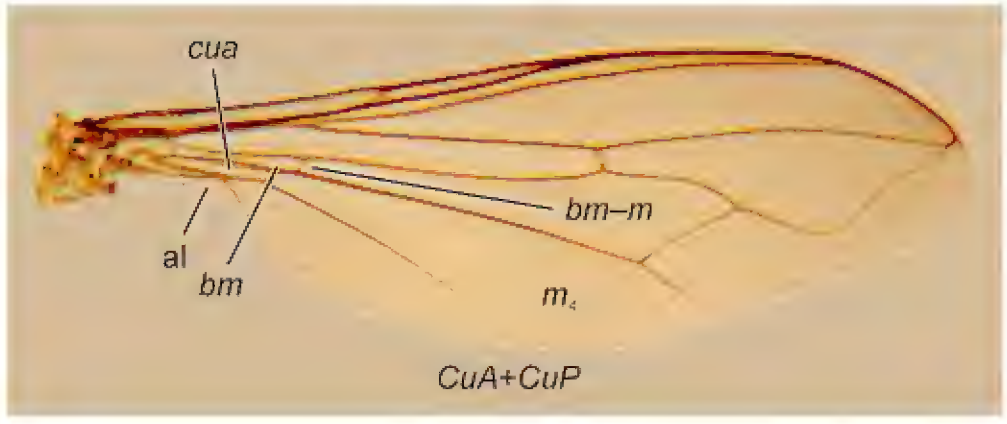
Traditionally, Conopidae have been divided into the subfamilies Conopinae, Dalmanniinae, Myopinae, Stylogastrinae and Zodioninae – a division that is, for example, implied in the historical work of Macquart (1835: 21), who divided all conopid species known to him into five genera: *Conops*, *Myopa* F., *Stachynia* Macquart (= *Dalmannia*), *Stylogaster* and *Zodion*. There has been some discussion concerning whether the Zodioninae should be treated as a subfamily or included within Myopinae, although recent investigations suggest the former is correct (Gibson *et al*. 2013). Gibson & Skevington (2013) introduced Sicinae as an additional subfamily, although the morphological synapomorphic characters which support this hypothesis are quite weak. It has been suggested that the Stylogastrinae represent a separate family, as first proposed by Séguy (1946) and accepted or advocated by subsequent authors, such as Marshall (2012: 314), Rohdendorf (1974: 108) and Smith & Cumming van Someren (1985). It is, however,



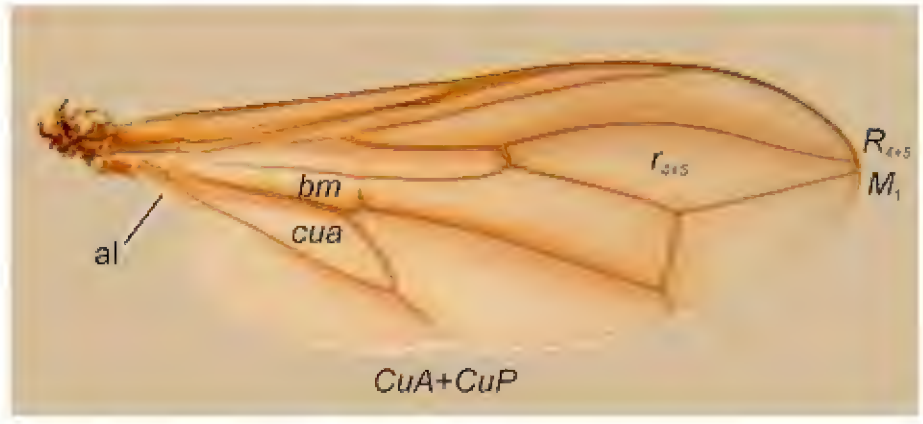
63 *Conops* (*Smithiconops*)



64 *Conops* (*Smithiconops*)



65 *Stylogaster*



66 *Pseudoconops*

Figs 66.63–66. Wings of Conopidae (dorsal views): (63) *Conops* (*Smithiconops*) *rondanii* Bezzi; (64) same, detail of mid wing section; (65) *Stylogaster westwoodi* Smith; (66) *Pseudoconops antennatus* Camras.

Abbreviations: A_1 – first branch of anal vein; al – alula; *bm* – basal medial cell; *bm–m* – basal medial crossvein; *br* – basal radial cell; *C* – costal vein; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *dm* – discal medial cell; *dm–m* – discal medial crossvein; fal vn – false vein; m_1 – first medial cell; M_1 – first branch of media; m_4 – fourth medial cell; M_4 – fourth branch of media; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; r_{4+5} – fourth + fifth radial cells; R_{4+5} – third branch of radius; $R_{4+5}+M_1$ – third branch of radius + first branch of media; *r–m* – radial–medial crossvein; *Sc* – subcostal vein; *sc–r* – subcostal–radial crossvein.

widely accepted that *Stylogaster* is the sister-group to the remainder of the Conopidae (e.g., Gibson & Skevington 2013) and the scientific case does not currently support either stance with any conviction. It is, therefore, more a question of taste whether to accept Stylogastrinae as a subfamily of Conopidae or as a separate family. As *Stylogaster* is traditionally treated within Conopidae, however, and because currently there is no compelling evidence for a change, the traditional family concept is retained here.

The division of the subfamilies into tribes has recently been reviewed by Gibson & Skevington (2013). These authors reorganised tribes based on a cladistic analysis at the global scale, but their definitions of tribes are not viable in some cases, and therefore, Stuke (2017: xiv) did not recognise any tribes in the world catalogue.

In addition, Schneider (2010) described the Australasian subfamily Notoconopinae, and for the few known fossil species, Camras (1994) erected the subfamily Palaeomyopinae.

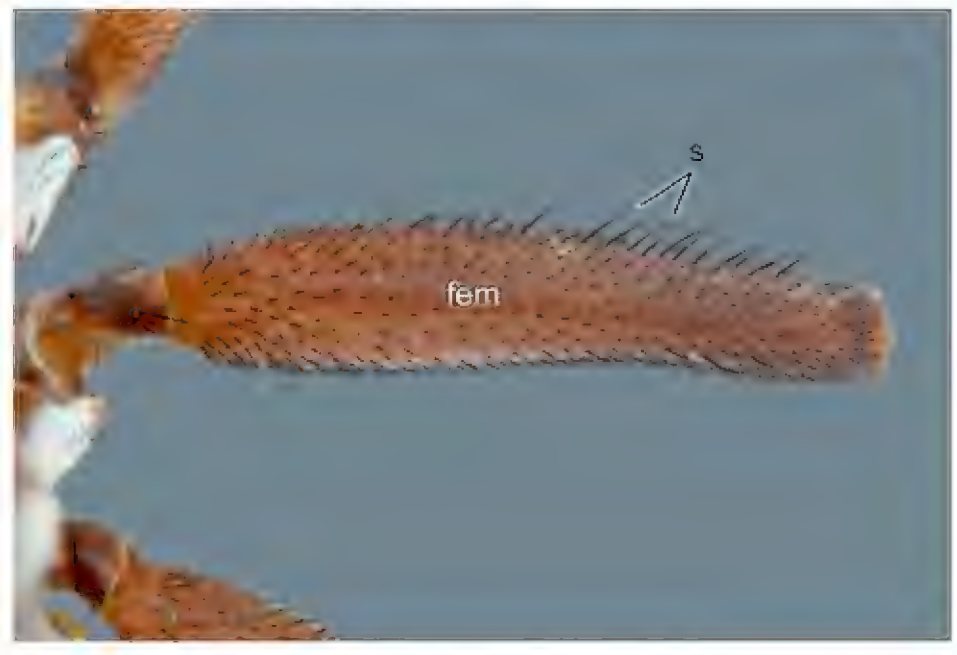
Identification

Diagnoses of the family Conopidae were provided by Gibson & Skevington (2013), Schneider (2010), Skevington *et al.* (2010:

67 *Paramyopa*

68 *Archiconops*

69 *Physocephala*



70 *Conops* (*Smithiconops*)

Figs 66.67–70. Scutellum, subscutellum and leg features of Conopidae: (67) scutellum of *Paramyopa oestracea* (Loew), dorsal view ♂; (68) scutellum and subscutellum of *Archiconops crypticus* Stuke, dorsal view ♀; (69) hind femur and tibia of *Physocephala antiqua* (Wiedemann), anterior view ♀; (70) mid femur of *Conops* (*Smithiconops*) *rondanii* Bezzi, dorsal view ♀.

Abbreviations: fem – femur; mtg – mediotergite; s – setulae; sct – scutum; sctl – scutellum; tb – tibia.

848) and Smith & Peterson (1987: 749) and important recent identification keys for schizophoran Diptera which include Conopidae were provided by Barraclough (1995), Buck *et al.* (2009: 115), Marshall *et al.* (2017: 308), McAlpine (1981: 105), Oosterbroek (2006: 49) and Papp & Schumann (2000: 184).

The most recent identification keys to adults of Afrotropical conopid genera were provided by Stuke (2012, 2015, 2019) and Stuke & Clements (2019). Identification of larvae is not possible at this time, due to the lack of descriptions of Afrotropical conopid larvae. Only the larvae of *Physocephala bimarginipennis* Karsch, 1887, *Stylogaster* cf. *westwoodi* and *S.* cf. *varifrons* have been described (Smith & Cumming-van Someren 1970, 1985). Even at the generic level it is not possible to identify larvae reliably from the region, as the larvae of several genera remain entirely unknown, although some Afrotropical genera were included in the partial larval identification keys provided by Konovalova & Zimina (1987: 48) and Smith (1966). A diagnosis of *Stylogaster* larvae was provided by Smith & Cumming-van Someren (1985). Conopidae are either direct-pinned or micro-pinned in the field for later double-mounting (see Chapter 2).

Key to genera of Afrotropical Conopidae

1. Head with facial carina distinctly protruding from mouth margin to antennal base (Fig. 38); without antennal grooves; setae invariably developed, not readily confused with setulae on head and thorax (Fig. 28); proboscis *ca* 2 × as long as head height (Fig. 38); prementum long, narrow, labellum obviously split apically for at least ⅓ length (Figs 60, 61), connected with prementum by moveable joint; wing (Fig. 65) with anterior cubital cell (*cua*) shorter than basal medial cell (*bm*); male terminalia (Figs 76–79) with obvious large surstylus; cercus longer than epandrium (Fig. 78); female without theca; female terminalia elongated to form ovipositor with two long cerci (Figs 90, 91) (STYLOGASTRINAE) . . . . . *Stylogaster* Macquart

– Head with facial carina at maximum protruding at mouth margin (e.g., Figs 33–37) and with antennal grooves (except in *Tropidomyia*); setae usually reduced, or easily confused with setulae on head and thorax (e.g., Figs 8–27); proboscis either with labellum not connected with prementum by moveable joint and *ca* 2 × as long as head height, or if labellum connected with moveable joint, then prementum broader and labellum not obviously split apically for *ca* ⅓ of length (e.g., Figs 59, 62); wing (e.g., Figs 63, 66), with anterior cubital cell (*cua*) distinctly longer than basal medial cell (*bm*) (except in *Dalmannia*); male terminalia (e.g., Figs 73–75, 80–85), with surstylus small, reduced or absent (except in *Zodion*); cercus shorter than epandrium; theca usually well-developed, female terminalia not ovipositor-like (e.g., Figs 15, 20, 22) (except *Anticonops* Kröber, *Dalmannia* and *Paramyopa* Kröber) and with inconspicuous, non-protruding cercus (e.g., Fig. 71) 2

2. Antennal arista stylate, inserted apically on postpedicel (e.g., Fig. 54); ocelli and ocellar tubercle reduced in several genera; short vertex separated on frons by more or less well-developed ridge (e.g., Figs 43, 45, 48); without ocellar triangle; lunule usually distinct (e.g., Figs 40–45); facial grooves reaching mouth opening, more or less divided by facial carina that widens and protrudes ventrally to form small facial tubercle (except in *Tropidomyia*) (e.g., Figs 34, 36); postgena not widened, not separate from small occiput (e.g., Figs 34, 36, 39); palpus reduced in several species; chaetotaxy reduced, with no obvious setae on head (e.g., Figs 34, 36); without preapical setae dorsally on tibiae; wing cell r_{4+5} petiolate, vein $R_{4+5}+M_1$ usually distinct (e.g., Fig. 63); subcostal–radial crossvein (*sc–r*) well-developed (e.g., Fig. 64); wing membrane may be partly bare of microtrichia; male terminalia with protandrium distinctly broader than epandrium, projecting over it (e.g., Figs 10–13); hypandrium sheath fused dorsally, entirely surrounding phallus; female tergite and sternite 5 fused (e.g., Fig. 87, except in *Anticonops*) (CONOPINAE) 3

– Antennal arista filiform, inserted dorsally on postpedicel (e.g., Fig. 56); ocelli not reduced, situated on ocellar tubercle; without short vertex separated from frons by transverse ridge, but long ocellar triangle may be present (e.g., Figs 47, 53); lunule indistinct, if developed at all; facial grooves not reaching mouth opening, only as far as broad ventral facial tubercle, or if reaching mouth opening, then not divided by distinct carina; postgena widened, separate from small occiput (e.g., Fig. 35); palpus not reduced (e.g., Fig. 62); chaetotaxy usually not reduced (but may be hard to discern between long body pile), always some setae on head; with preapical setae dorsally on tibiae (in *Dalmannia* setae may be absent); wing cell r_{4+5} open, or if closed, then vein $R_{4+5}+M_1$ short; subcostal–radial crossvein (*sc–r*) undeveloped (e.g., Fig. 66, except in *Zodion*); wing membrane entirely clothed in microtrichia; male terminalia with protandrium not obviously broader than epandrium, not projecting over it (e.g., Fig. 17); hypandrium sheath not fused dorsally, not entirely surrounding phallus; female tergite and sternite 5 not fused 17

3. Head with face without grooves, but with protruding carina (Fig. 39); 2 lateral ocelli and ocellar tubercle present (as in Fig. 50); antennal arista with 2 articles . . . . . *Tropidomyia* Williston

– Head with face with grooves, without protruding carina (e.g., Figs 34, 36, 37); ocelli and ocellar tubercle absent in most genera (e.g., Figs 43–45); antennal arista with 2–3 articles (e.g., Figs 54, 57, 58) 4

4. Antennal postpedicel short, *ca* as long as high (Fig. 9); ocellar tubercle with at most 2 indistinct lateral ocelli; ptilinal fissure not extending beneath antennal bases; head without shiny pruinescence (Fig. 9); wing vein R_1 terminating in costal vein (*C*) at middle of termination of subcostal vein (*Sc*) and vein R_{2+3}; male terminalia with hypoproct evident, but not projecting out of epandrium; female tergite and sternite 5 not fused laterally (not recorded from Afrotropical Region) . . . . . [*Brachyceraea* von Röder]

– Antennal postpedicel long, distinctly longer than high (e.g., Figs 54, 57, 58); ocellar tubercle with ocelli only present in a few genera (e.g., Figs 49, 50); ptilinal fissure extending beneath antennal bases (e.g., Figs 34, 36, 37); head, e.g., on gena or eye margin, distinctly shiny pruinescent; wing veins R_1 and R_{2+3} terminating close together at costal vein (*C*), well beyond end of subcostal vein (*Sc*) (e.g., Fig. 63); male terminalia with hypoproct not evident; female tergite and sternite 5 fused laterally (e.g., Fig. 87) 5

5. Proboscis weakly sclerotised and soft, much shorter than head length (Fig. 16); labellum short, entirely divided, at least 2 × broader than adjacent prementum, with *ca* 15 pseudotracheae on each labellum; legs with posterior surfaces of fore and mid tibiae without obvious pruinescence fields distally (as in Fig. 16); basal ⅓ of mid femur posteriorly without regularly arranged, long setulae; fore coxa with 1–4 black setae stronger than surrounding scattered setulae; female anterior surface of theca with a few black setulae apically (not recorded from Afrotropical Region) . . . . . .[*Leopoldius* Rondani]

– Proboscis usually well-sclerotised, at least as long as head length (e.g., Figs 34, 36, 37); labellum elongate, usually not entirely divided, usually as broad as adjacent prementum (e.g., Fig. 59), with < 10 pseudotracheae on each labellum (except in *Pleurocerinella* Brunetti); legs with posterior surfaces of fore and mid tibiae with obvious pruinescence fields distally (e.g., Figs 10, 11, 26); basal ⅓ of mid femur posteriorly with regularly arranged long setulae in several genera; fore coxa without black setae stronger than surrounding scattered setulae; female anterior surface of theca usually without black setulae apically 6

6. Antennal postpedicel very long, at least 2 × as long as pedicel (e.g., Figs 36, 37) 7

– Antennal postpedicel at maximum *ca* as long as pedicel (e.g., Fig. 34), usually distinctly shorter (e.g., Fig 10). 9

7. Compound eye with unique horn-like projection on occiput near posterior margin of eye (Fig. 36); lunule indistinct (Fig. 46); black, metallic shiny species, with obvious orange tip to abdomen, orange postpronotum and orange tip to scutum (Fig. 15); thorax with katepisternum shiny, without pruinescent fascia (Fig. 15); mediotergite shiny black; scutum and scutellum with obvious strong setae, as on notopleuron or postalar callus . . . . . .*Euconops* Kröber

– Compound eye without unique horn-like projection at hind margin (e.g., Fig. 37); lunule more or less distinct (e.g., Figs 49, 52); species differently coloured (e.g., Figs 24, 29); thorax with katepisternum with pruinescent fascia; mediotergite orange, brown or black, always pruinescent, not shiny; scutum and scutellum without setae or with setula-like setae only. 8

8. Head without black fronto-orbital maculae (Fig. 49); dark black to brown species (Fig. 24); parafacial with long black setulae (Fig. 24); labellum markedly broader than prementum, with distinct setulae (Fig. 37); thorax with scutum entirely clothed in black setulae, *ca* as long as diameter of base of tibiae (Fig. 24). . . . . .*Pleurocerinella* Brunetti

– Head with distinct black fronto-orbital maculae (Fig. 52); light orange-brown species with contrasting black legs (Fig. 29); parafacial without black setulae (Fig. 29); labellum barely broader than prementum, with inconspicuous, short setulae only; thorax with scutum with only scattered black setulae, distinctly shorter than diameter of base of tibiae (Fig. 29) . . . . . *Tammo* Stuke

9. Thorax with proepisternum without proepisternal seta ventrally above fore coxa; wing with radial–medial crossvein (*r–m*) positioned well beyond middle of discal medial cell (*dm*); mid femur at most with indistinct row of long, regularly arranged black setulae on posterior surface; hind femur sometimes widened in basal ½ (Fig. 69) . . . . . *Physocephala* Schiner

– Thorax with proepisternum with at least 1 long, black proepisternal seta ventrally above fore coxa; wing with radial–medial crossvein (*r–m*) at most positioned only slightly beyond middle of discal medial cell (*dm*); mid femur invariably with row of long, regularly arranged black setulae on posterior surface (e.g., Fig. 70); hind femur not obviously widened in basal ½. 10

10. Female abdomen without distinct protruding theca (Fig. 7); sternite 5 not fused with tergite 5; sternites 5 and 6 with only scattered, irregularly arranged, short, black setae, covering only small area of sternites; female tergite 7 *ca* 2 × as long as height of tergite 6, markedly elongate; tergite 6 markedly narrower than tergite 3; [only the unique female holotype of one *Anticonops* species known (Fig. 7); the following characters may facilitate determination of males: frons without transverse grooves, with only indistinct anterior longitudinal grooves; frons with black fronto-orbital maculae; face without pruinescence, except for narrow pruinescent fascia along eye margin; facial grooves pruinescent; thorax orange-brown, with indistinct

black scutum; legs orange-red, with only tarsi blackish; with indistinct silver-grey pruinescent fascia from mid coxa to anepisternum, not reaching scutum; without setae on katepisternum or scutellum; wing membrane entirely clothed in microtrichia, brownish with slightly darker brown colouration in anterior part, between costal vein (*C*), vein R_{4+5} and cell r_{4+5}; abdomen orange-red] . . . . . *Anticonops* Kröber

– Female abdomen with distinct protruding theca (e.g., Figs 20, 22); sternite and tergite 5 fused with each other; sternites 5 and 6 with fields of dense black setae, covering entire surface (may be regularly arranged); female tergite 7 at most slightly longer than height of tergite 6, not elongate; tergite 6 *ca* as broad as tergite 3; [males not with combination of characters listed above for *Anticonops*] 11

11. Head with ocellar tubercle with ocelli well-developed (e.g., Figs 40, 42, 50); vertex not separated from frons by ridge (e.g., Figs 40, 42, 50) 12

– Head without either ocellar tubercle or ocelli absent (e.g., Figs 41, 43–45); vertex separated from frons by more or less distinct arching ridge (e.g., Figs 41, 43–45). 14

12. Head with gena entirely silvery pruinescent (Fig. 40); frons orange-brown, with black fronto-orbital macula and additional pair of dark maculae above (Figs 6, 40); wing membrane slightly brownish to hyaline, with only cell r_{2+3} brownish apically (Fig. 6); legs orange-brown to brown; abdomen not obviously elongate (Fig. 6) . . . . . *Aegloconops* Gibson

– Head with gena only partly silvery pruinescent; frons more or less black, at most with fronto-orbital macula only (e.g., Figs 42, 50); wing membrane with different pattern of dark colouration; legs more or less black, especially tarsi usually black (e.g., Figs 10, 26); abdomen elongate (e.g., Figs 10, 26) 13

13. Head with ocellar tubercle elongate, with distinct triangular vertex (Fig. 42); 3 ocelli present (may be difficult to discern); palpus very short but distinct, with black setae; antennal arista with medial aristomere not extended ventrally, apical aristomere with obvious broadened base (Fig. 57); wing membrane (Fig. 10) without distinct darker anterior margin, cell r_{2+3} entirely dark, not contrasting with basal radial cell (*br*); basal medial cell (*bm*) and anterior cubital cell (*cua*) mostly clothed in microtrichia; thorax with postpronotum black (Fig. 10); female abdomen with theca narrow, triangular, with posterior surface clothed in black spines apically, not arrange in rows (Fig. 5) . . . . . *Caenoconops* Kröber

– Head with ocellar tubercle not elongate, without distinct triangular vertex (Fig. 50); 2 lateral ocelli present; palpus absent; antennal arista with medial aristomere extended ventrally, apical aristomere without obvious broadened base (Fig. 58); wing membrane (Fig. 26) with anterior margin entirely brownish, cell r_{2+3} entirely brown, contrasting with lighter basal radial cell (*br*); basal medial cell (*bm*) mainly without microtrichia, anterior cubital cell (*cua*) without microtrichia basally; thorax with postpronotum orange-brown to dark brown (Fig. 26); female abdomen with theca broad, posterior surface almost entirely clothed in black spines, arranged in rows. . . . . *Schedophysoconops* Gibson

14. Head with vertex markedly swollen (Fig. 41); frons without grooves; wing with radial–medial crossvein (*r–m*) positioned distinctly more basal than subcostal–radial crossvein (*sc–r*) and medial crossvein (*dm–m*) in line with distal section of vein M_1; membrane usually entirely tinged blackish brown (may exhibit violet reflection in fresh specimens) (Fig. 8); thorax with mediotergite markedly bulging (Fig. 68); male tergite and sternite 5 fused . . . . . *Archiconops* Smith

– Head with vertex not markedly swollen (Figs 43–45); frons with grooves in most species (Figs 43, 45); wing with radial–medial crossvein (*r–m*) not positioned more basal than subcostal–radial crossvein (*sc–r*) in most species and discal medial crossvein (*dm–m*) and distal section of vein M_1 not in line (Fig. 63); membrane not usually entirely infuscate (without violet reflection in fresh specimens); thorax with mediotergite not markedly bulging; male tergite and sternite 5 not fused . . . . *Conops* L. *sensu lato* 15

15. Head with vertex with fine longitudinal grooves anteriorly (Fig. 45); frons with small transverse grooves anteriorly (Fig. 45); compound eye with posterior margin convex, without more or less distinct shiny notch (Fig. 34); wing vein $R_{4+5}+M_1$ short, distinctly shorter than radial–medial crossvein (*r–m*); right-angle between discal medial crossvein (*dm–m*) and medial portion of vein M_1 (Fig. 63); antennal postpedicel *ca* as long as pedicel (Fig. 54); female abdomen with anterior margin of tergite 7 without notch. . . . . *Conops* (*Smithiconops* Camras)

– Head with vertex without fine longitudinal grooves anteriorly (e.g., Figs 43, 44); frons with, or without, transverse grooves; compound eye with posterior margin straight to slightly concave, usually with more or less distinct shiny notch; wing vein $R_{4+5}+M_1$ *ca* as long as radial–medial crossvein (*r–m*); other characters variable 16

16. Head with frons with transverse grooves (Fig. 43); female abdomen with anterior margin of tergite 7 with notch . . . . . *Conops* (*Asiconops* Chen)

– Head with frons smooth, without transverse grooves (Fig. 44); female abdomen with anterior margin of tergite 7 without notch. . . . . *Conops sensu stricto*

17. Labellum short, not connected to basal proboscis by moveable joint; wing with subcostal–radial crossvein (*sc–r*) (as in Fig. 64); male terminalia with hypoproct obviously elongate, slightly sclerotised, clothed in microtrichia, projecting out of epandrium; posterior and anterior surstyli well-developed; hypandrial bars not fused distally; hypandrium sheath only slightly sclerotised, barely evident; distiphallus with small dorsal sclerotisation and two smaller, less distinct lateral sclerotisations (ZODIONINAE) . . . . . *Zodion* Latreille

– Labellum long, connected to basal proboscis by moveable joint (e.g., Fig. 62); wing without subcostal–radial crossvein (*sc–r*) (e.g., Fig. 66); male terminalia with hypoproct not evident; posterior and anterior surstyli reduced or small (e.g., Fig. 83); hypandrial bars fused distally (e.g., Fig. 84); hypandrium sheath usually sclerotised (except in *Sicus*); distiphallus with different pattern of sclerotisation if evident 18

18. Wing with anterior cubital cell (*cua*) *ca* as long as basal medial cell (*bm*); head without obvious setae amongst pile (Fig. 14); thorax with conspicuous subscutellum, virtually as high as mediotergite; abdominal tergite 1 largely membranous anteriorly; male terminalia with distiphallus elongate, *ca* 2 or 3 × longer than epandrium, winding, laterally sclerotised, with long setulae; female abdomen without theca, but with ovipositor-like structure; most species with obvious yellow-black abdominal colouration (Fig. 14) (not recorded from Afrotropical Region) (DALMANNIINAE) . . . . . [*Dalmannia* Robineau-Desvoidy]

– Wing with anterior cubital cell (*cua*) distinctly longer than basal medial cell (*bm*) (e.g., Fig. 66); head with several setae, more or less obvious amongst pile (e.g., Fig. 47); thorax with inconspicuous subscutellum, much smaller than mediotergite; abdominal tergite 1 not membranous anteriorly; male terminalia with distiphallus not markedly elongate, with different structure (e.g., Fig. 85); female abdomen with theca well-developed, without ovipositor-like structure (except in *Paramyopa*); never with yellow-black abdominal colouration (MYOPINAE) 19

19. Thorax with proepisternum setulose dorsally; antennal arista 1-articled; male terminalia with hypandrial membrane with obvious setae 20

– Thorax with proepisternum not setulose dorsally; antennal arista 1-, 2- or 3-articled (e.g., Fig. 56); male terminalia with hypandrial membrane without obvious setae 22

20. Antennal arista markedly white in apical ½; head with gena distinctly broader than ½ eye height (Fig. 17), without black setulae; face convex in lateral view, without protruding mouth margin; facial grooves extending ventrally from antennal bases for *ca* ½ of face length only; fore and mid tibiae without rows of short, thick adpressed black setae on ventral surface basally (not recorded from Afrotropical Region) . . . . . [*Melanosoma* Robineau-Desvoidy]

– Antennal arista entirely brown; head with gena at most only slightly broader than ½ eye height (e.g., Figs 25, 30), with scattered black setulae; face concave in lateral view, with protruding mouth margin; facial grooves extending from antennal bases to mouth opening; fore and mid tibiae with more or less distinct row of short, thick adpressed black setae on the ventral surface basally 21

21. Antennal pedicel and postpedicel slightly longer than head length, length of scape *ca* 4 × longer than greatest width (Fig. 25); arista narrowing uniformly, without distinctly broader base; abdominal tergite 2 elongate, distinctly longer than tergites 3 and 4 combined (confined to Madagascar) . . . . . *Pseudoconops* Camras

– Antennal pedicel and postpedicel shorter than head length, length of scape at most 2 × longer than greatest width (Fig. 30); arista with distinctly broader basal part, becoming abruptly narrower towards apex; abdominal tergite 2 not elongate, at most as long as tergites 3 and 4 combined (continental Afrotropics and Madagascar) . . . . . *Thecophora* Rondani

22. Head with gena *ca* ½ eye height (Fig. 27); subcostal wing vein (*Sc*) reaching costal vein (*C*) well before apex of vein R_1; antennal arista 1-articled; thorax with prosternum broad, oval; male terminalia with hypandrial sheath barely sclerotised, indistinct; distiphallus *ca* as long as epandrium, with obvious strips of sclerotised microtrichia and area of strong black setae (not recorded from Afrotropical Region) . . . . . [*Sicus* Scopoli]

– Head with gena broader than ½ eye height (e.g., Fig. 35); subcostal wing vein (*Sc*) reaching costal vein (*C*) at apex of vein R_1; antennal arista 2- or 3-articled (e.g., Fig. 56); thorax with prosternum reduced to narrow sclerotised strip; male terminalia with hypandrial sheath sclerotised, distinct; distiphallus shorter than epandrium, with different pattern of microtrichia and setae, if present (widespread Afrotropical Region) 23

23. Scutellum without submedial patches of dense black setulae and medial depression; wing with cell r_{4+5} either open or closed; halter knob without silver pruinescence; female abdomen tip not elongate or forming ovipositor-like structure . . . . . *Myopa* F.

– Scutellum with 2 submedial patches of dense black setulae (Fig. 67), with a setose depression between; wing cell r_{4+5} open widely; halter knob with obvious silver pruinescence; female abdomen tip elongate, forming ovipositor-like structure. . . . . *Paramyopa* Kröber

Synopsis of the fauna

The world fauna of Conopidae currently comprises *ca* 779 valid species in 56 genera. About 156 valid conopid species are known to date from the Afrotropical Region in 17 genera. The conopid fauna of the Afrotropics is a very distinct one, with only a few species, such as *Conops* (*Asiconops*) *elegans* Meigen, 1824 and *Physocephala antiqua* (Wiedemann, 1830), being widespread both in the Afrotropics and extending farther north into southern Europe and the Arabian Peninsula. Conversely, species with distributions mainly in the Palaearctic are only rarely reported from the Afrotropics, such as *Myopa stigma* Meigen, 1824 (Stuke 2013), *M. buccata* (L., 1758) (Kröber 1916) and *Conops* (*C.*) *flavicauda* Bigot, 1880 (Camras 1962). Probably eight of the 17 genera known from the Afrotropics are endemic. Biogeographical hotspots can scarcely be identified due to wide variations in collector effort in the different countries sampled. Most records published to date are from South Africa (46 species), Democratic Republic of the Congo (46 species), Kenya (41 species) and Madagascar (36 species). Madagascar is outstanding, however, with 34 of 36 species endemic, containing a very high proportion of the described Afrotropical *Stylogaster* species (25 of the 42 Afrotropical valid species described to date).

***Aegloconops* Gibson** (Conopinae)**.** An endemic monotypic genus, with the single described species, *A. quadripunctatus* (Kröber, 1915) (Figs 2, 6), widely distributed in the Afrotropical Region. Biology and immature stages of the species remain unknown.

***Anticonops* Kröber** (Conopinae)**.** An endemic monotypic genus, with the single described species, *A. abdominalis* (Kröber, 1936), described from Democratic Republic of Congo. The species is only known from a single female specimen (Fig. 7) and identification of males remains doubtful. Biology and immature stages of the species remain unknown.

***Archiconops* Kröber** (Conopinae)**.** A genus of 10 described species (Fig. 8), occurring in the Afrotropical, Oriental and Palaearctic Regions. Six species occur in the Afrotropical Region which are widely distributed in the eastern half of the continental Afrotropics, together with records from Madagascar, South Africa, Tanzania and Uganda. Stuke (2004) revised the world species of this small genus and additional comments were provided by Camras (2007) and Stuke (2019). Biology and immature stages remain unknown. Stuke (2004) provided an identification key that includes all six Afrotropical species.

[***Brachyceraea* von Röder** (Conopinae)**.** A monotypic Palaearctic genus with the single described species, *B. brevicornis* (Loew, 1847) (Fig. 9), reported from Syria by Kröber (1915). The genus has not been reported from the Afrotropical Region, but could potentially occur there. Biology and immature stages of the species remain unknown.]

***Caenoconops* Kröber** (Conopinae)**.** An endemic genus of two described species: *C. bicolor* (Kröber, 1931) (Fig. 10), recorded from Burundi, Ethiopia, Lesotho, Mozambique, Nigeria, South Africa and Zimbabwe; and *C. freidbergi* Camras, 2000, described from Kenya. Biology and immature stages remain unknown. Camras (2000) and Stuke (2019) discussed the identification of the two species and Stuke (2019) presented an identification key.

***Conops* L.** (Conopinae)**.** A genus of 120 described species (Figs 3, 11–13), occurring in all zoogeographical regions, except Antarctica. Thirty described species are recorded from the Afrotropical Region, divided into three subgenera: *C.* (*Asiconops* Chen) (Fig. 11), *C.* (*Conops* L.) (Fig. 12) and *C.* (*Smithiconops* Camras) (Fig. 13). The subgenus *C.* (*Asiconops*) is distributed throughout the continental Afrotropics and is also widespread in the Australasian, Oriental and Palaearctic Regions, but is not recorded from the New World. As numerous *Conops* species are not currently assigned to subgenus, it is not possible to provide a reliable number of species globally at the current time. In the Afrotropical Region, however, some 18 valid *C.* (*Asiconops*) species are known. Stuke (2019) published an identification key to Afrotropical species. The subgenus *Conops sensu stricto* is mainly distributed in the Palaearctic Region and the occurrence of this taxon in other zoogeographical regions is difficult to assess, as many of the described *Conops* species are of unknown subgeneric position. Eight Afrotropical species belong to the subgenus. These species are distributed throughout almost the entire Afrotropical Region. Only one predominantly Palaearctic species of *Conops sensu stricto* is known from the Afrotropics to date: *C.* (*C.*) *flavicauda*, reported from Uganda by Camras (1962). The identification of Afrotropical species in the subgenus *Conops sensu stricto* was summarised by Stuke (2019). The Afrotropical subgenus *C.* (*Smithiconops* Camras) (Fig. 13) is widely distributed in the region, with four valid species described to date. These species can be identified with the identification key provided by Stuke (2019). The only known host record of an Afrotropical *Conops* is that of *C.* (*A.*) *unicolor* Kröber, 1915, associated with *Campsomeris erythrogaster* Saussure (Moutia & Mamet 1946), *Cathimeris lachesis* (Saussure) (Herting & Simmonds 1977: 119) and *Micromeriella pilosella* (Saussure) (all Hymenoptera: Scoliidae) (Moutia & Mamet 1946; Stuke 2019). Elsewhere *Conops* infests a wide range of aculeate Hymenoptera hosts, including species of Apidae, Pompilidae, Scoliidae, Sphecidae and Vespidae.

[***Dalmannia* Robineau-Desvoidy** (Dalmanniinae)**.** A genus of 12 described species (Fig. 14), occurring in the Nearctic and Palaearctic Regions. The distributions of two Palaearctic *Dalmannia* species extend into North Africa. The genus is not recorded from the Afrotropical Region, but may be recorded from the region in the future. Almost all of the few host records for *Dalmannia* are from the closely related Apidae genera *Halictus* Latreille and *Lasioglossum* Curtis.]

***Euconops* Kröber** (Conopinae)**.** An endemic monotypic genus, with the single described species, *E. bellus* Kröber, 1915 (Fig. 15), described from South Africa. Biology and immature stages of the species remain unknown.

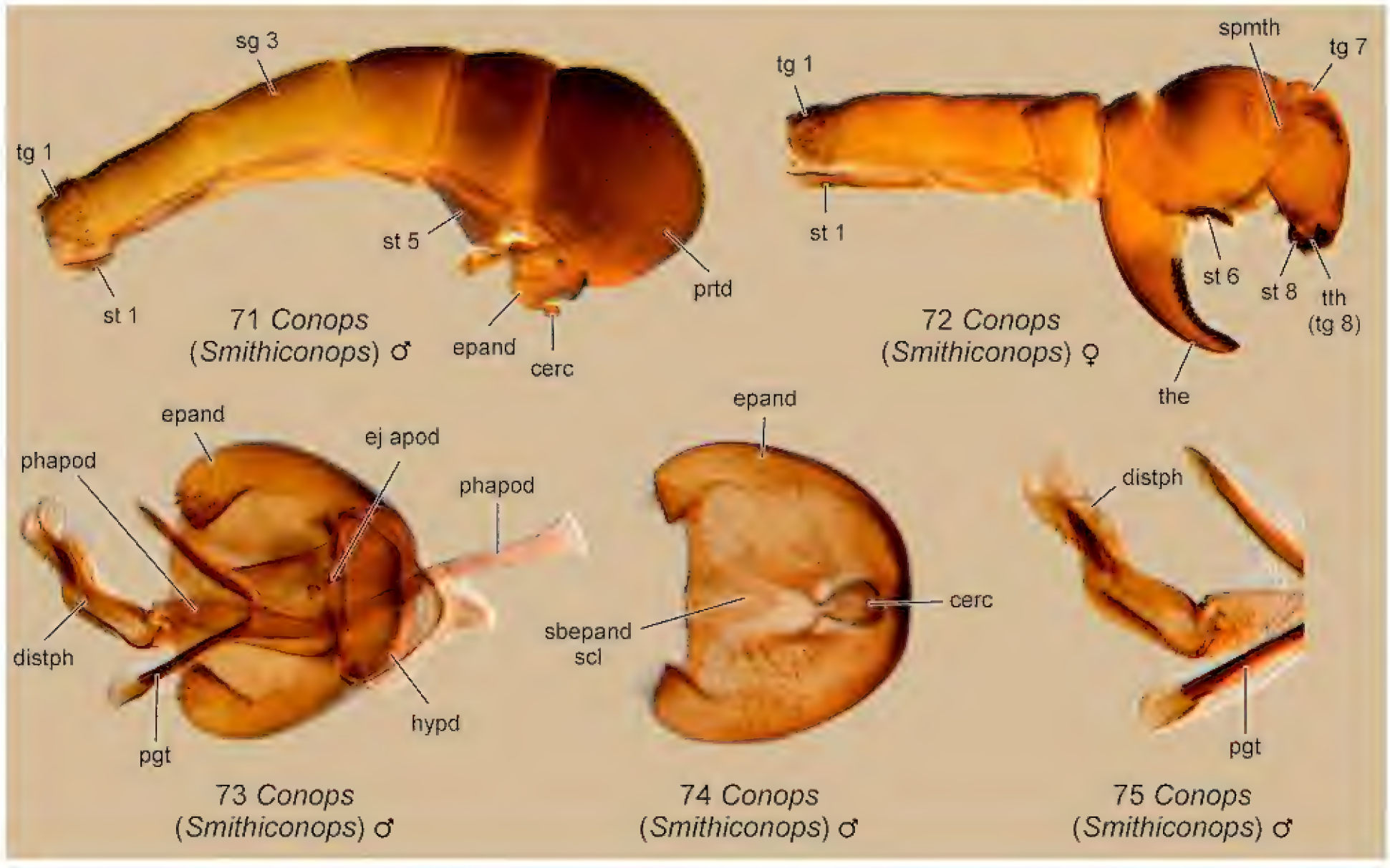
[***Leopoldius* Rondani** (Conopinae)**.** A genus of nine described species (Fig. 16), occurring in the Palaearctic Region. The records of *L. coronatus* (Rondani, 1857) (Fig. 16) from Morocco (Séguy 1930) and *L. anatolii* Zimina, 1963 and *L. calceatus* (Rondani, 1857) from Tunisia (Clements & Vincent 2001; Kröber 1914) in Palaearctic North Africa, are the only African records of the genus. The genus has not been recorded to date from the Afrotropical Region, but could potentially occur there. The few known host records of *Leopoldius* are from Vespidae.]

[***Melanosoma* Robineau-Desvoidy** (Myopinae)**.** A genus of four described species (Fig. 17), occurring in the Oriental and Palaearctic Regions. Two Palaearctic species are reported from North Africa: *M. bicolor* (Meigen, 1824) (Fig. 17) from Algeria, Morocco and Tunisia (Becker 1907; Kröber 1924; Séguy 1941) and *M. mundum* Czerny & Strobl, 1909, from Algeria and Morocco (Becker & Stein 1913; Séguy 1930, 1949; Stuke & Schmid-Egger 2016). The genus has not been recorded to date from the Afrotropical Region, but could potentially occur there. Biology and immature stages remain unknown.]

***Myopa* F.** (Myopinae)**.** A genus of 44 described species (Fig. 18), occurring in all zoogeographical regions, except Antarctica. About ten Palaearctic species are reported from North Africa, but only *M. picta* Panzer, 1798 and *M. stigma*, which occur in Ethiopia, are recorded in the Afrotropics (Stuke 2013). All of the reliable host records of *Myopa* are from several genera of Apidae. The identification of Afrotropical *Myopa* species is possible using the works of Chvála (1965), Clements (2000), Stuke (2002) and Stuke & Clements (2008).

***Paramyopa* Kröber** (Myopinae)**.** An endemic genus of three described species (Figs 4, 19). The distribution of these is disjunct, with *P. insignis* (Jaennicke, 1867) being recorded once only from Ethiopia, *P. oestracea* (Loew, 1863) (Fig. 19) recorded from Lesotho, Namibia and South Africa and *P. clementsi* Stuke, 2021 recorded from South Africa. Biology and immature stages remain unknown. The most recent identification key is that of Stuke (2015) supplemented by Stuke (2021).

***Physocephala* Schiner** (Conopinae)**.** A genus of 130 described species (Figs 20–23), occurring in all zoogeographical regions except Antarctica. Forty-five species occur in the Afrotropical Region, being distributed throughout. Stuke & Clements (2019) recently synonymised the genera *Dacops* Speiser and *Pseudophysocephala* Kröber with *Physocephala*

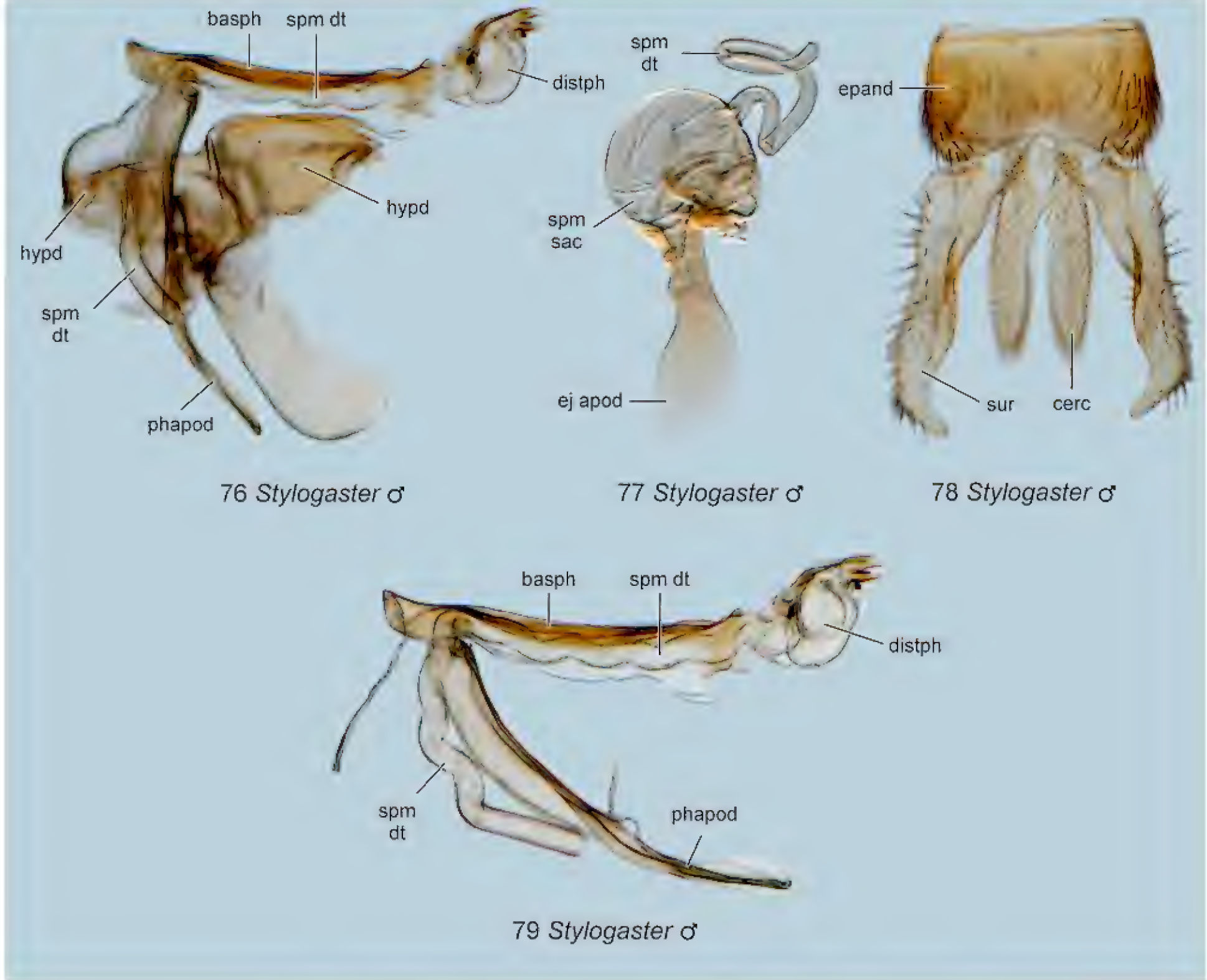


Figs 66.71–75. Abdomens and male terminalia of Conopidae: (71) abdomen of *Conops* (*Smithiconops*) *rondanii* Bezzi, lateral view ♂; (72) same ♀; (73) same, male terminalia, ventral view; (74) same, epandrium, ventral view; (75) same, distiphallus, dorsal view.

Abbreviations: cerc – cercus; distph – distiphallus; ej apod – ejaculatory apodeme; epand – epandrium; hypd – hypandrium; pgt – postgonite; phapod – phallapodeme; prtd – protandrium; sbepand scl – subepandrial sclerite; sg – segment; spmth – spermatheca; st – sternite; tg – tergite; the – theca; tth – tooth.

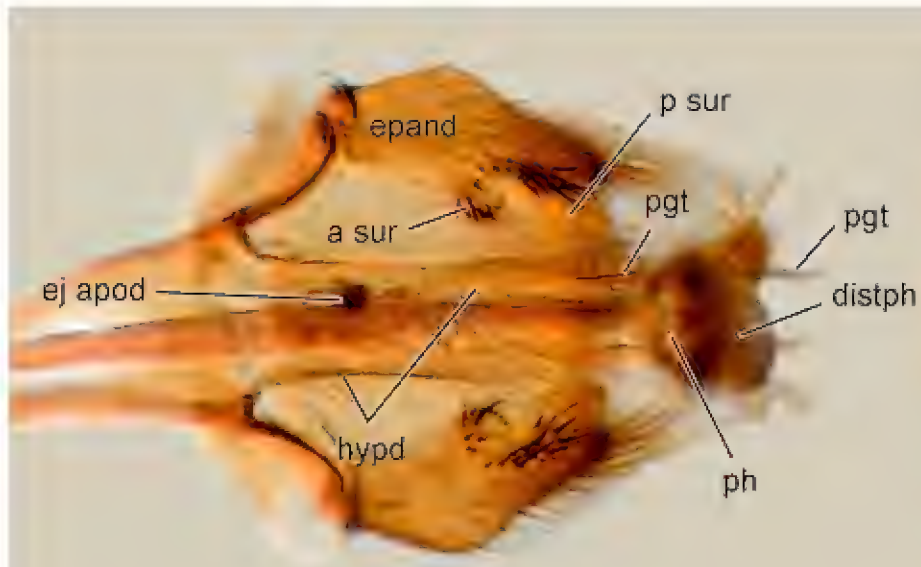
and as a result, the genus is now by far the most species-rich genus in the Afrotropical Region. In addition, there are several Palaearctic species recorded from North Africa, but these records require further evaluation. There are some published reports of bee hosts for Afrotropical *Physocephala*: *P. abdominalis* (Kröber, 1915) with *Apis mellifera* L. (Johannsmeyer 2001: 210); *P. bimarginipennis* with *Xylocopa caffra* (L.) (Watmough 1974), *X. erythrina* Gribodo (Watmough 1974), *X. flavorufa* (DeGeer) (Smith & Cunningham-van Someren 1970; Stuke & Clements 2019; Watmough 1974), *X. hottentotta* Smith (Smith & Cunningham-van Someren 1970; Watmough 1974), *X. nigrita* (F.) (Watmough 1974), *X. rufa* Friese (Stuke & Clements 2019), *X. scioensis* Gribodo (Watmough 1974) and *X. senior* Vachal (Watmough 1974); *P. pubescens* Brunetti, 1925 with *Apis mellifera ligustica* Spinola (Chorley 1936); *P. tetratarsata* (Camras, 2001) with "bees" (Camras 2001; Stuke & Clements 2019); and *P. vitripennis* Curran, 1928 with *A. mellifera adansoni* Latreille (Camras 2001; Mei 1999). Almost all *Physocephala* host records are from Apidae. Due to the large size of *Physocephala* it is not surprising that large Apidae, such as *Anthophora* Latreille, *Bombus* Latreille, *Centris* F., *Megachile* Latreille and *Xylocopa* Latreille, are most regularly reported as hosts. An identification key to Afrotropical species was presented by Stuke & Clements (2019).

***Pleurocerinella* Brunetti** (Conopinae)**.** A genus of nine described species (Fig. 24), occurring in the Afrotropical, Oriental and Palaearctic Regions. Five species occur in the Afrotropics, widely distributed from Kenya in the north-east to Namibia and South Africa in the south. Biology and immature stages



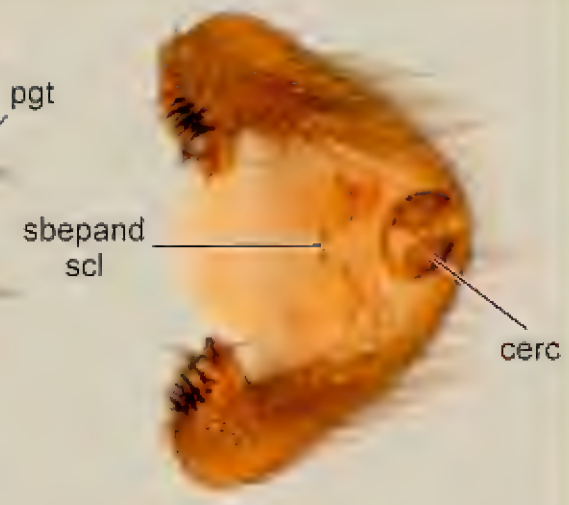
Figs 66.76–79. Male terminalia of Conopidae: (76) hypandrium and phallus of *Stylogaster westwoodi* Smith, lateral view; (77) same, sperm pump, lateral view; (78) same, epandrium, dorsal view; (79) same, phallus, lateral view.

Abbreviations: basph – basiphallus; cerc – cercus; distph – distiphallus; ej apod – ejaculatory apodeme; epand – epandrium; hypd – hypandrium; phapod –phallapodeme; spm dt – sperm duct; spm sac – sperm sac; sur – surstylus.

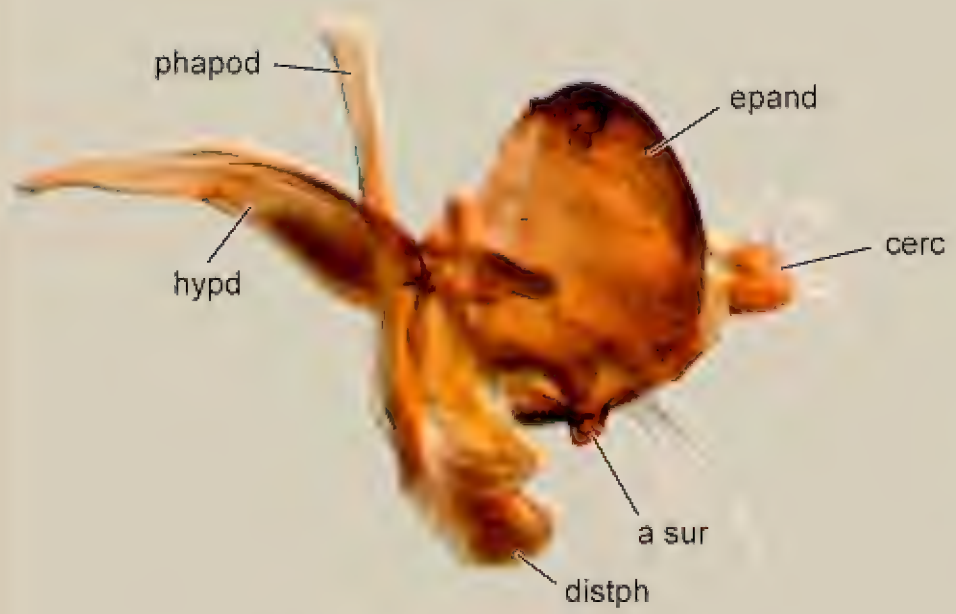


80 *Paramyopa* ♂

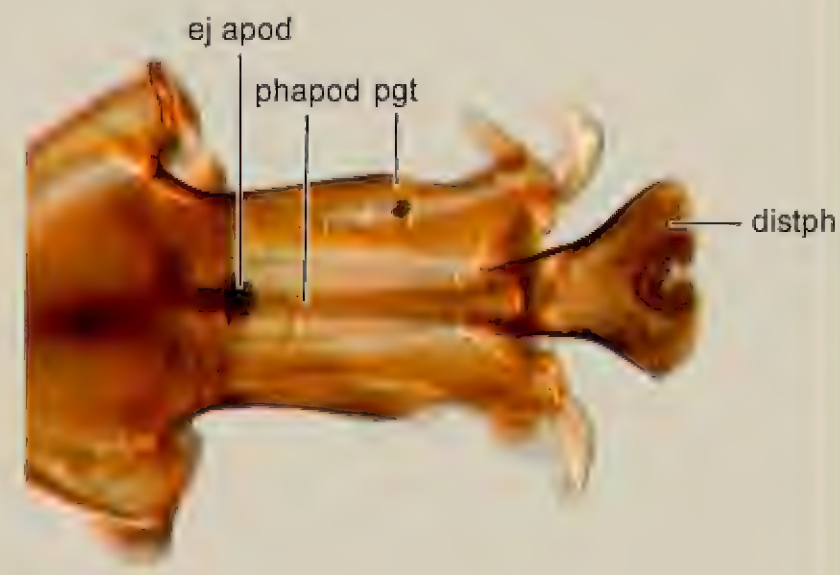
81 *Paramyopa* ♂



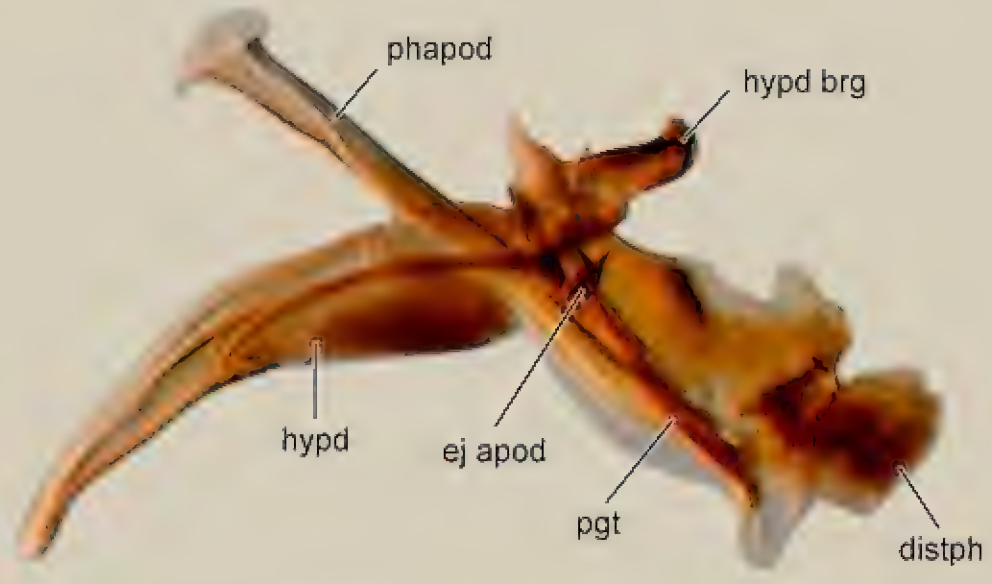
82 *Paramyopa* ♂



83 *Pseudoconops* ♂



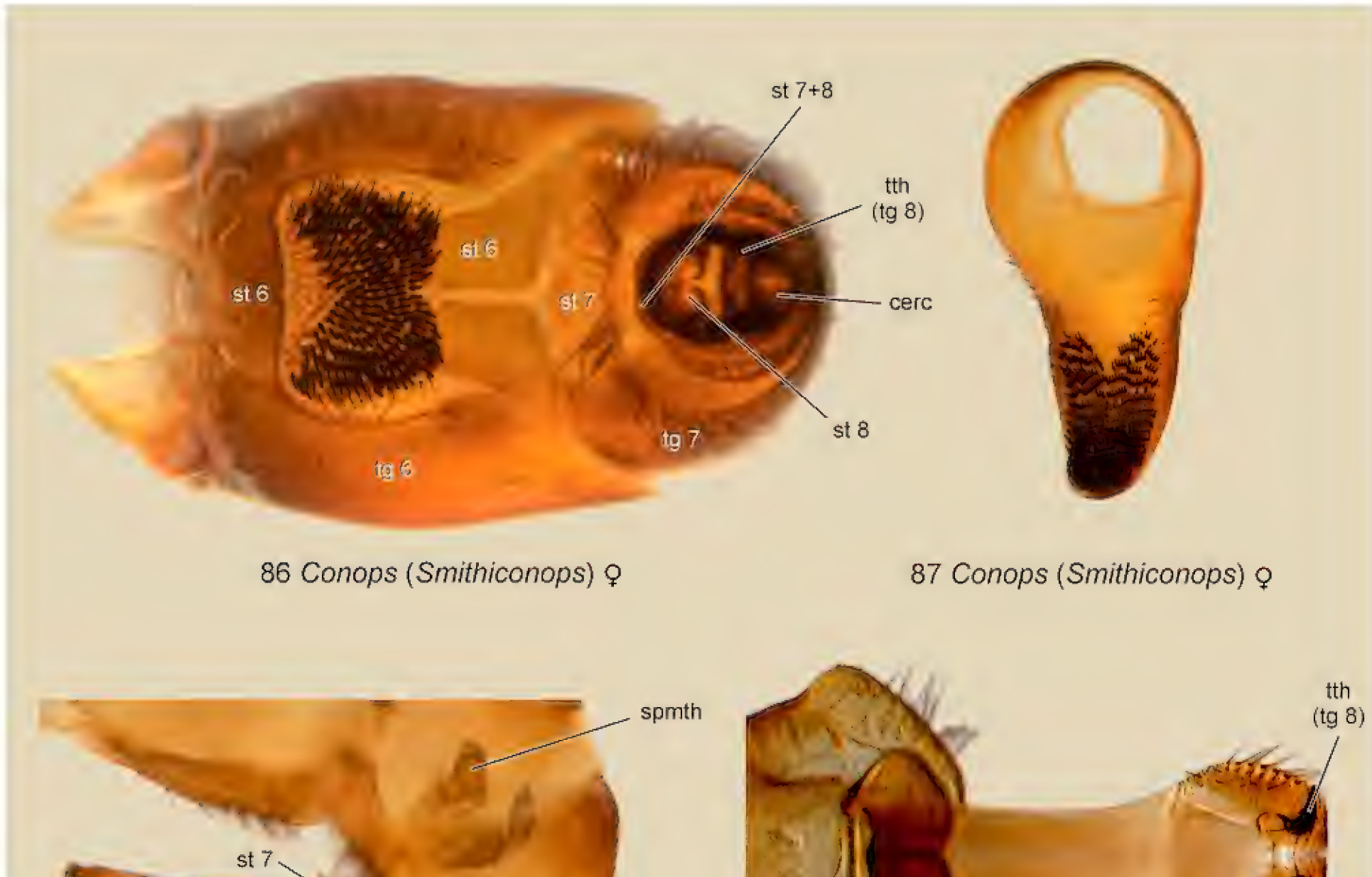
84 *Pseudoconops* ♂



85 *Pseudoconops* ♂

Figs 66.80–85. Male terminalia of Conopidae: (80) terminalia of *Paramyopa oestracea* (Loew), ventral view; (81) same, tip of phallus dorsal view; (82) same, epandrium, posterodorsal view; (83) terminalia of *Pseudoconops antennatus* Camras, lateral view; (84) same, hypandrium and distiphallus, ventral view; (85) same, hypandrium and phallus, lateral view.

Abbreviations: a sur – anterior surstylus; cerc – cercus; distph – distiphallus; ej apod – ejaculatory apodeme; epand – epandrium; hypd – hypandrium; hypd brg – hypandrial bridge; p sur – posterior surstylus; pgt – postgonite; ph – phallus; phapod – phallapodeme; sbepand scl – subepandrial sclerite.



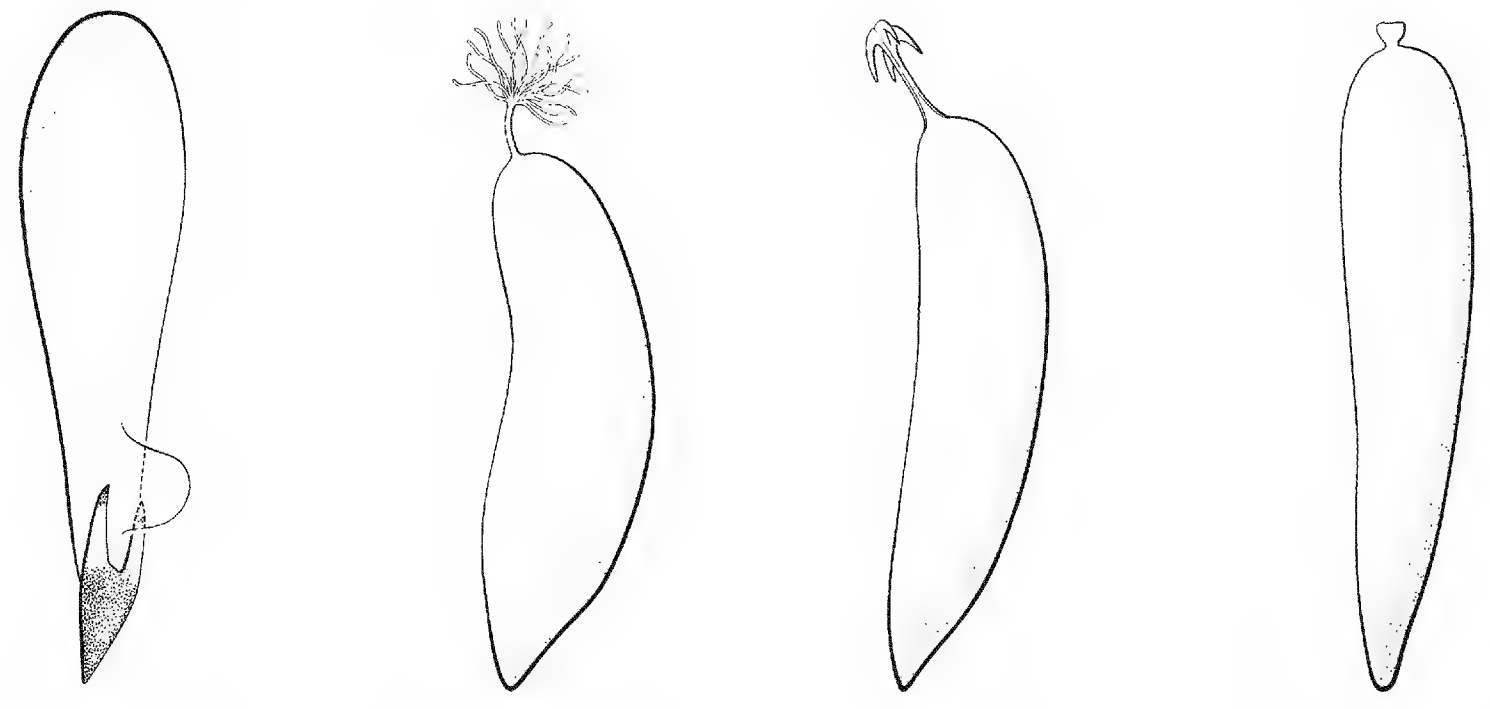
Figs 66.86–91. Female terminalia of Conopidae: (86) tip of the abdomen of *Conops* (*Smithiconops*) *rondanii* Bezzi, ventral view; (87) same, segment 5 including theca, posterior view; (88) tip of the abdomen of *Physocephala abdominalis* (Kröber), lateral view; (89) same, spoon-shaped structure, ventral view; (90) abdomen of *Stylogaster westwoodi* Smith, dorsolateral view; (91) same, terminalia, lateral view.

Abbreviations: cerc – cercus; epiprct – epiproct; hyprct – hypoproct; lat lb – lateral lobe; spmth – spermatheca; st – sternite; tg – tergite; tth – tooth.

92 *Stylogaster*

93 *Stylogaster*

94 *Stylogaster*



95 *Stylogaster* 96 *Conops* (*Conops*) 97 *Myopa* 98 *Dalmannia*

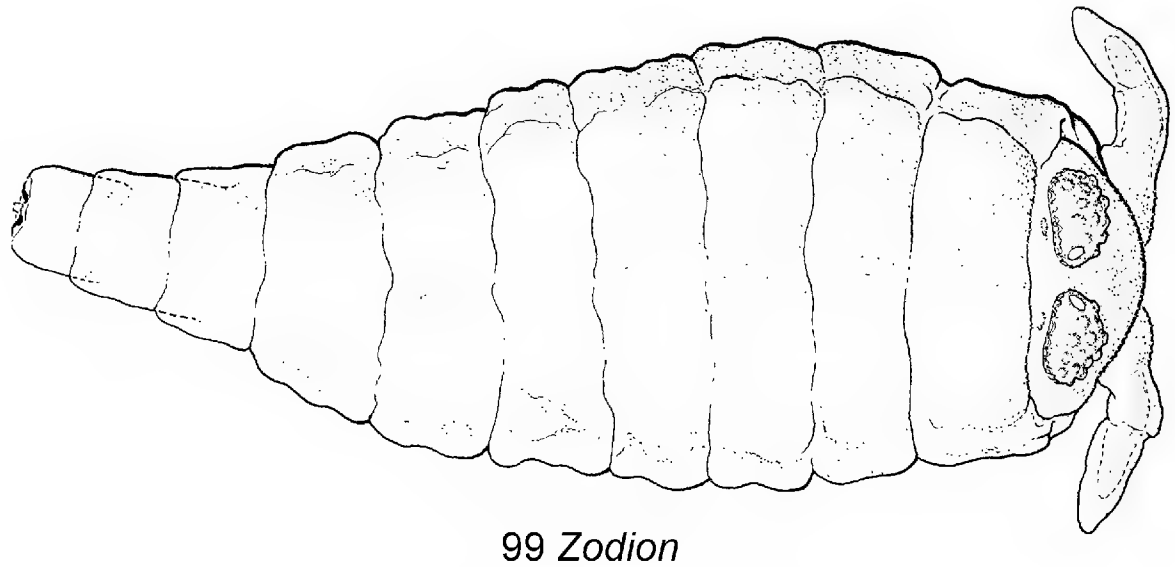
Figs 66.92–98. Eggs of Conopidae and eggs impaled in Diptera hosts: (92) egg of *Stylogaster westwoodi* Smith, lateral view; (93) head of *Afromydaea debilis* (Stein) (Muscidae), impaled by two *Stylogaster* eggs (arrowed); (94) same, thorax of *Coenosia ruwenzorica* (Emden) (Muscidae), with one egg (arrowed); (95) egg of *Stylogaster biannulata* (Say), lateral view (non-Afrotropical); (96) same, *Conops* (*Conops*) *flavipes* L. (non-Afrotropical); (97) same, *Myopa buccata* (L.) (non-Afrotropical); (98) same, *Dalmannia punctata* (F.) (non-Afrotropical). Figs 93, 94 (Couri *et al*. 2013, figs 1, 2), Figs 95–98 (Smith & Peterson 1987, figs 25–28).

remain unknown. These species can be identified using the identification key provided by Stuke (2009, 2019).

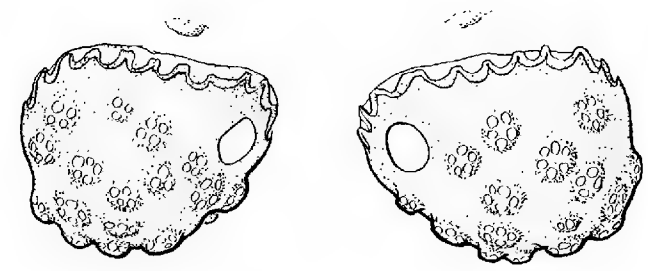
***Pseudoconops* Camras** (Myopinae)**.** An endemic monotypic genus, with the single described species, *P. antennatus* Camras, 1962 (Fig. 25), confined to Madagascar. Biology and immature stages of the species remain unknown.

***Schedophysoconops* Gibson** (Conopinae)**.** An endemic monotypic genus, with the single described species, *S. longicornis* (Kröber, 1915) (Fig. 26), widely distributed in Central, East and Southern Africa. Biology and immature stages of the species remain unknown.

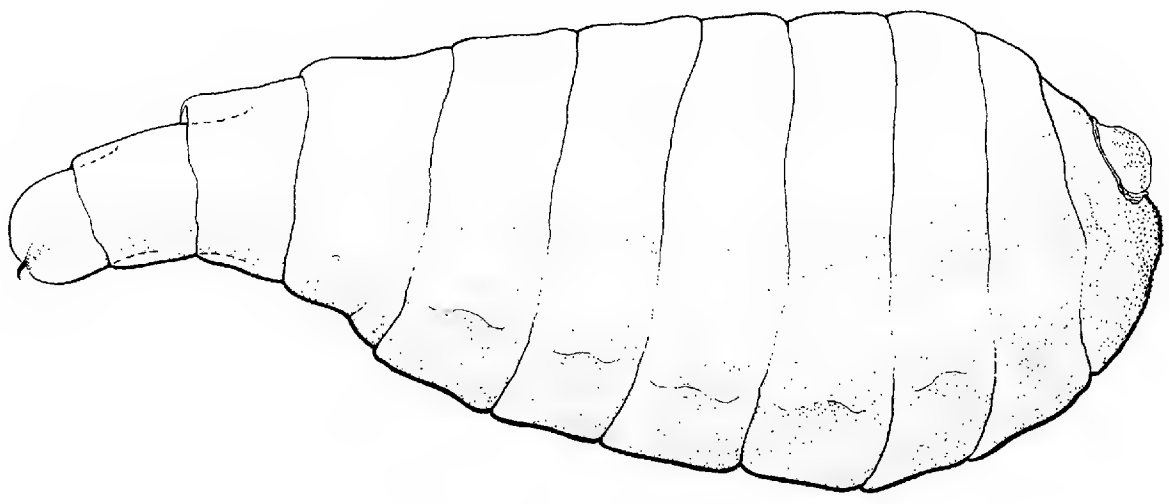
[***Sicus* Scopli** (Myopinae)**.** A genus of nine described species (Fig. 27), occurring in the Oriental and Palaearctic Regions. The Palaearctic species *S. ferrugineus* (Fig. 27) is recorded from Morocco to Syria in Palaearctic North Africa. The genus has not been recorded to date from the Afrotropical Region. Confirmed host records for *Sicus* are restricted to various bumblebees (*Bombus*) and these do not occur in the Afrotropical Region.]



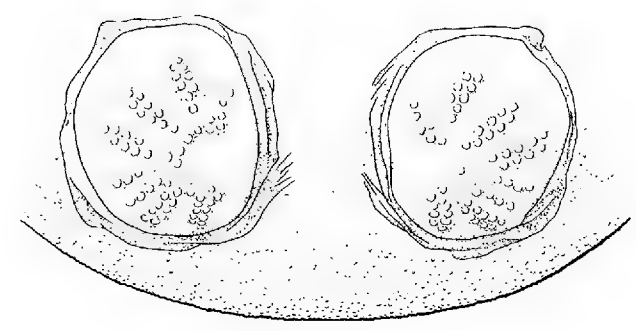
99 *Zodion*



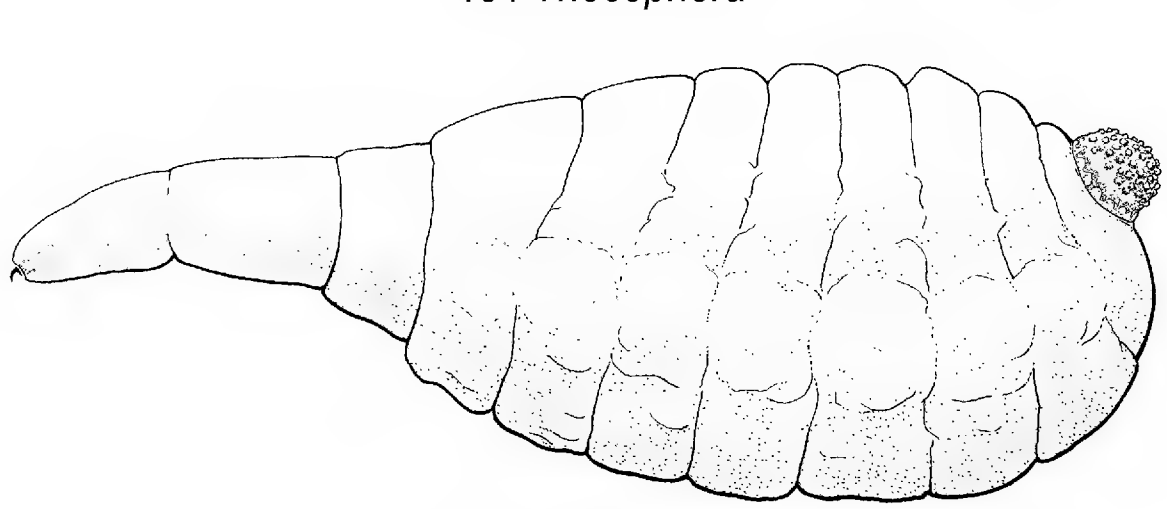
100 *Zodion*



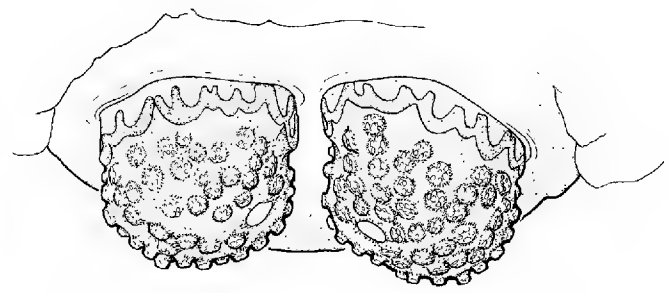
101 *Thecophora*



102 *Thecophora*



103 *Physocephala*



104 *Physocephala*

Figs 66.99–104. Immature stages of Conopidae: (99) larva of *Zodion* sp., dorsal view (non-Afrotropical); (100) same, posterior spiracles, caudal view; (101) larva of *Thecophora* sp., lateral view (non-Afrotropical); (102) same, posterior spiracles, caudal view; (103) larva of *Physocephala bimarginipennis* Karsch, lateral view (non-Afrotropical); (104) same, posterior spiracles, caudal view. Figs 99–104 (Smith & Peterson 1987, figs 19–24).

***Stylogaster* Macquart** (Stylogastrinae)**.** A genus of 125 described species (Figs 1, 28), occurring in all zoogeographical regions, except Antarctica. Forty-five species are recorded from the Afrotropical Region, but numerous undescribed species are still anticipated. The genus is widespread in the region, with records from Côte d'Ivoire to Nigeria in Central Africa and Ethiopia in the north-east, to Madagascar and South Africa in the south. Madagascar has a distinct fauna, with some 25 endemic species, none of which occur in the continental Afrotropics. Examination of the male terminalia (e.g., Figs 76–79), is essential for the identification of species and most females cannot be identified reliably, other than by direct association with males. Published hosts records of *Stylogaster* are discussed in detail above. Immature stages of some Afrotropical *Stylogaster* have been described by Smith & Cunningham-van Someren (1985). The publications of Smith (1967) and Stuke (2012, 2015) facilitate identification of the species recorded to date.

***Tammo* Stuke** (Conopinae)**.** An endemic monotypic genus, with the single described species, *T. rufus* (Camras, 1955) (Fig. 29), recorded from Kenya and Mozambique. Biology and immature stages remain unknown.

***Thecophora* Rondani** (Myopinae)**.** A genus of 40 described species (Figs 5, 30), occurring in all zoogeographical regions, except Antarctica. Some undescribed species are also known from the Oriental and Palaearctic Regions. Ten species are recorded from the Afrotropics and are widely distributed in the region, with Palaearctic species occurring north of the Sahara and an almost entirely different fauna in sub-Saharan Africa. Only one Palaearctic species is known to occur as far south as Ethiopia and the five Palaearctic species recorded from North Africa require confirmation. It can be assumed that the whole region, including Madagascar, is populated with *Thecophora* species, which are not as obvious as other Conopidae and, therefore, are often under-represented in collections. The Afrotropical fauna therefore appears poorer than is probably the case. Almost all host records for the genus *Thecophora* are from the Apidae genera *Halictus* and *Lasioglossum*. Stuke (2015) published an identification key to the Afrotropical species.

***Tropidomyia* Williston** (Conopinae)**.** A genus of six described species (Fig. 31), occurring in all zoogeographical regions, except the Australasian Region and Antarctica. Two species occur in the Afrotropics: *T. africana* Camras, 2001, recorded from Benin, Kenya and South Africa and *T. ornata* Kröber, 1915 (Fig. 31), recorded throughout the Afrotropical Region: another species occurs in nearby Israel. Biology and immature stages remain unknown. Afrotropical *Tropidomyia* species can be identified using the identification key provided by Stuke (2019).

***Zodion* Latreille** (Zodioninae)**.** A genus of 62 valid species (Fig. 32), occurring in the Afrotropical, Nearctic, Neotropical, Palaearctic and Oriental Regions. Two species occur in the Afrotropics: the Palaearctic *Z. cinereum* (F., 1794), recorded from Central African Republic (Stuke 2015); and the endemic *Z. perbellum* Speiser, 1909 (Fig. 32), recorded from Ethiopia, Kenya and Tanzania (Camras 2001). Given the size of the genus it is remarkable that there is only one endemic species known to date from the Afrotropics. All host records of *Zodion* are from Apidae of various genera. *Zodion perbellum* has unique colouration (Fig. 32) and can be readily identified using the original description by Speiser (1909). Palaearctic species that occur in North Africa, and the remaining Afrotropical species, can be identified using the identification key provided by Mei & Stuke (2008).

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LONCHAEIDAE 67

(Lance Flies)

Iain MacGowan and Graham E. Rotheray

Fig. 67.1. Female of *Lonchaea* sp. (non-Afrotropical) (photograph © S.A. Marshall).

Diagnosis

Small-sized (body length: 3–6 mm), stout-bodied acalyptrate flies (Fig. 1), with broad wings, long, usually shiny blue-black (metallic blue-green in *Lamprolonchaea* Bezzi and *Fulgenta* MacGowan); head wide and high; thorax broad; abdomen broad and flat; wing usually hyaline, occasionally fumose or with apical darkening, but never patterned; halter invariably black.

Head (Fig. 2), with compound eye large, round to high oval in profile, usually bare, occasionally pilose as in *Dasiops aethiopicus* McAlpine, 1964 and several undescribed sub-montane *Lonchaea* Fallén species; frons narrower in male than in female, strongly sclerotised and setulose, without lateral setae; orbital plates reaching ¼–⅓ distance from vertex to lunule; lunule large (Fig. 2), exposed and bare (*Earomyia* Zetterstedt, *Fulgenta* and *Lamprolonchaea*) or setulose (*Dasiops* Rondani, *Lonchaea* and *Silba* Macquart); face broad, depressed, usually without strong facial carina or antennal grooves; 1 reclinate fronto-orbital seta present (Fig. 2); ocellar and inner and outer vertical setae strong (Fig. 2); postocellar setae divergent, rather weak; gena below eye (Fig. 2) with 1 to several rows of setulae; no distinct vibrissa present, but occasionally (*Dasiops* and some *Silba* species), 1 or more genal setulae enlarged and seta-like; antenna with postpedicel (Fig. 2) short and prominent, to long and decumbent, black, but often orange-brown basally and/or ventrally; arista (Fig. 2) bare to pubescent or plumose; palpus moderately large, relatively broad and flattened at apex.

Thorax with mesonotum (Fig. 3) rather strongly arched, pruinescent to highly polished; setae and setulae fairly dense and strong; 1 postpronotal seta, 1 presutural supra-alar seta, 2 notopleural setae, 1 postsutural supra-alar seta, 2 postalar setae, 2 postsutural dorsocentral setae and 2 prescutellar acrostichal setae present; a weak postsutural intra-alar seta frequently present; proepisternum with 1 seta; proepimeron with 1 setula (some *Dasiops* exceptionally with 2–5 setulae); anterior

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marginal portion of anepisternum, directly above, and slightly posterior to prothoracic spiracle, with (*Dasiops*), or without (all other genera) poststigmatal seta or setae; anepisternum with numerous setae and setulae, sometimes without anterodorsal setae, but these invariably present on posterior margin; katepisternum with 1–2 strong setae dorsocentrally and numerous setulae; anepimeron bare; meron bare; prosternum usually bare, sometimes with a few fine setulae laterally; metasternal area bare. Scutellum with 4 marginal setae, *i*.e., lateral and apical pair, with or without additional setulae at margins, apex or on disc. Wing (Fig. 4) rather strongly tapered from base to apex, *i*.e., anal lobe and alula well-developed; costal vein (*C*) extended to vein M_1, constricted, but not entirely broken at position of humeral and subcostal breaks; subcostal vein (*Sc*) complete and free from vein R_1; pterostigmal section (between insertions of veins *Sc* and R_1), 1–3 × length of *r–m* crossvein; cells *bm* and *dm* separated; cell *cua* present; vein *CuA+CuP* extending to (or close to) wing margin as a fold or not; membrane usually hyaline, but occasionally yellowish to dark fumose, rarely with apical darkening; upper calypter well-developed, with whitish to blackish margins and fringes, of uniform length in described Afrotropical species; halter normally entirely blackish (brownish in *Silba eximia* McAlpine, 1964 from Madagascar). Legs stout, coxae, femora, and tibiae blackish (dark brown in some *Silba* species); tarsi black, but often with basal tarsomeres yellowish; femora rather swollen, with numerous setae and setulae; tibiae with numerous rows of setulae, but very few if any setae; preapical dorsal seta usually indistinguishable, except occasionally on mid tibia; apicoventral seta present on mid tibia.

Abdomen broad and flat; 7 pairs of spiracles in membrane adjacent to respective tergites and sternites; male terminalia (Figs 5–14), with tergite 6 present in *Dasiops*, otherwise absent, or indistinguishably fused with tergite 5; sternite 6 varying from well-developed, symmetrical, separate and in ventral position, to reduced, asymmetrical, fused with sternites 7 and 8 and shifted to laterodorsal position on left side; epandrium, hypandrium and associated structures usually symmetrical; hypandrium in *Dasiops* (Figs 5, 6), relatively simple; pregonite rudimentary usually in form of pair of broad, low blades; postgonites weakly developed, membranous lobes near base of phallus; phallapodeme usually rudder-shaped, projecting from anterior margin of hypandrium; in other genera hypandrium more complex (Figs 7–12), pregonites usually in form of pair of arms or rods; postgonite reduced, semi-membranous, to strongly developed and toothed; relatively large, horizontal, plate-like hypandrial apodeme arising anteriorly from anterior margin of hypandrium; vertical, blade-like anterior portion of phallapodeme fused along midline of hypandrial apodeme; posterior margin of phallapodeme divided vertically, with each side expanded laterally to form phallic guide which is variable in shape and complexity; some species-groups within *Lonchaea* with postgonites present on either side of phallus, often long and complex; surstylus articulated with lateral margins of epandrium, pendulant in *Dasiops* (Figs 5, 6), at least partially enclosed within lateral margins of epandrium in other genera (Figs 7–14), with (Figs 5, 6, 13, 14), or without (Figs 7–12), strong prensisetae; phallus short, unsegmented and spout-like in *Dasiops* (Figs 5, 6), to elongate, bi-segmented into basiphallus and distiphallus and ornamented in other genera (Figs 7–14); cerci in form of simple lobes, usually flap-like, variously sclerotised and setulose; female terminalia with sclerotised telescopic ovipositor (Figs 15, 16), abdominal sternite 6 and occasionally sternite 5 with median anteriorly directed apodeme arising from anterior margin; oviscape composed of laterally fused tergite and sternite 7, broadly conical in shape, with dorsal and ventral pair of long strap-like extensions extending posteriorly, which can be withdrawn into abdomen and into which retracted aculeus is located; aculeus in form of 4 elongate rods, derived from tergite and sternite 8, broad and blade-like in several *Dasiops* species (Fig. 15), occasionally in *Silba*, but elongate and narrow in *Lamprolonchaea* (Fig. 16), *Fulgenta* and *Lonchaea*; apical sclerite formed by fusion of epiproct, hypoproct and cerci, variously shaped, often setulose and in some genera, especially *Dasiops*, of considerable value in species recognition; 3 spermathecae present, usually elongate and wrinkled, but sometimes bell-shaped or spherical and smooth.

Adult Lonchaeidae superficially resemble some small Muscidae (see Chapter 113), but are separable by the absence of a complete transverse suture on the mesonotum. They are sometimes confused with Agromyzidae (see Chapter 86), but differ in having a longer discal medial cell (*dm*) (shorter than distal section of vein M_1 in Agromyzidae). The metallic blue-green species of the genera *Lamprolonchaea* and *Fulgenta* may resemble representatives of several other acalyptrate families, but the black halter and lack of setae on the tibiae are good diagnostic features.

Biology and immature stages

Larvae of Lonchaeidae are associated with a wide range of plant material. Species in the genera *Lamprolonchaea*, *Lonchaea* and *Silba* have been reared from various fruits, either as primary or secondary invaders and have potential to be of economic significance. Other *Silba* species have been recorded from decay in the stems of plants, such as Sugarcane, *Saccharum* spp. (Poaceae). Afrotropical species of *Dasiops* are more associated with grassland habitats, where several species have been recorded as forming galls on grass (Poaceae) stems, in which the larvae develop. In overall terms, little is known regarding the larval biology of Afrotropical species. The strong association of the majority of Nearctic and Palaearctic *Lonchaea* with dead wood micro-habitats is unknown at present in the Afrotropical Region.

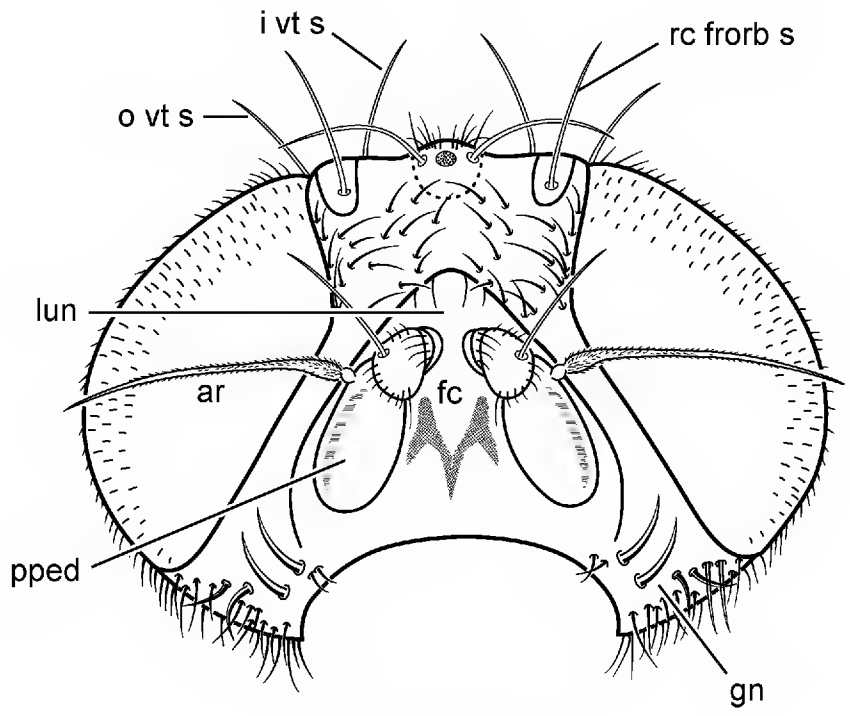
Adult lonchaeids are unusual amongst acalyptrates, in that they form aerial mating swarms and such behaviour has been observed in all Afrotropical genera. The large eyes and broad thorax, containing large flight muscles, are adaptations for this form of mating behaviour. Otherwise, lonchaeids are often relatively slow-moving, females usually being observed or captured at their preferred oviposition sites, males being less frequently encountered, unless obtained from reared material; sex ratio of reared specimens being usually 1 : 1.

The best documented immature stages are from the Northern Hemisphere, particularly those in the genera *Dasiops* and *Lonchaea* (*e.g.*, Ferrar 1987: 205; Krivosheina 1976: 250; MacGowan & Rotheray 2008; Morge 1959, 1962). Lonchaeid larvae utilise a diversity of plant parts and a range of feeding modes, including saprophagy, zoophagy and phytophagy. As a result, lonchaeid larvae exhibit great diversity in the form and

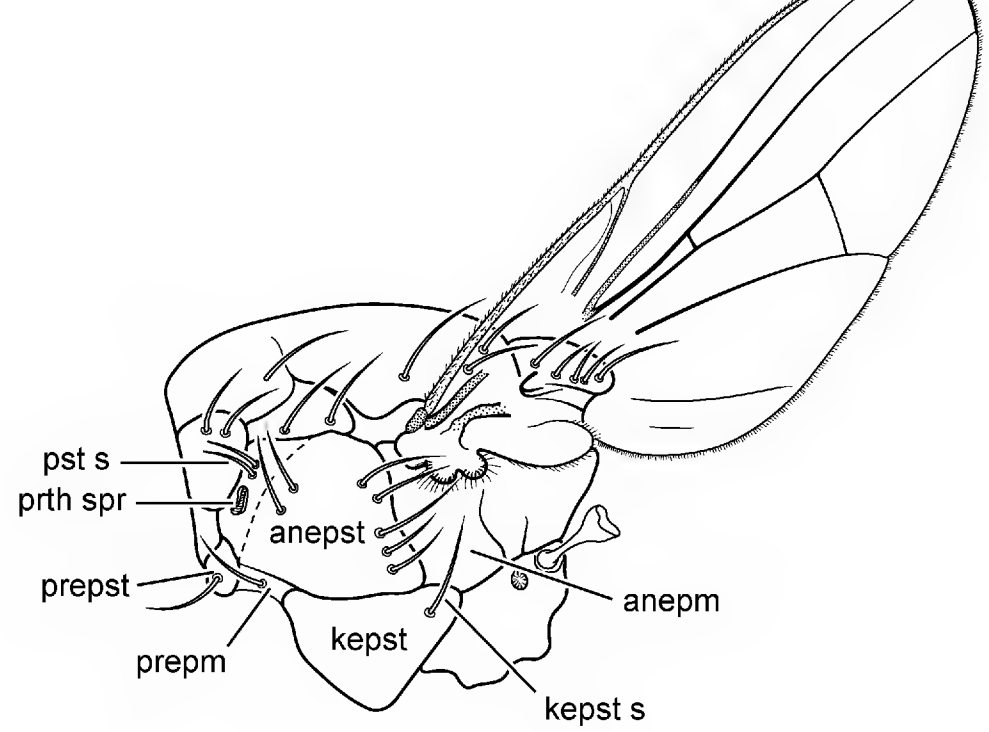
feeding mechanisms. So much so that it is difficult to establish a character or characters in combination that readily distinguish lonchaeid larvae and puparia.

Based on an examination of larvae and puparia of the genera *Dasiops*, *Earomyia*, *Lamprolonchaea*, *Lonchaea* and *Silba*, a start towards defining a family-level set of larval and puparial distinguishing characters may include the following: basal sclerite of cephaloskeleton with black sclerotisation, mostly confined to the anterior end of the basal sclerite and dorsal cornu (Figs 19–22); creeping welts with seven transverse rows of spicules, which vary in size and arrangement (Fig. 17 indicates five rows, as the remaining spicular rows are too small to illustrate); posterior spiracles (Fig. 18) on upper margin, not the centre, of the apex of abdominal segment 8 and borne on basal projections, usually black, sometimes red or brown, often with apical or other projections of great variety and form.

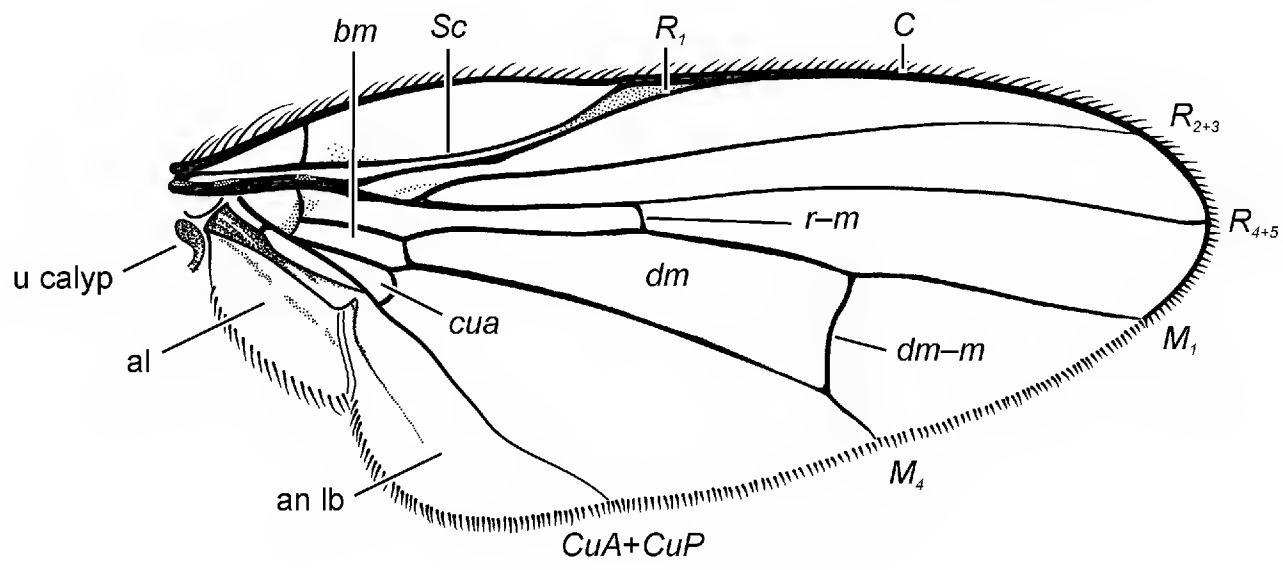
The pseudocephalon and prothorax are especially variable. The fleshy pseudocephalon (Fig. 22), consists of two parallel lobes, each of which ensheaths a mouthhook and on the dorsal side the maxillary palpus (not depicted in Fig. 22), while



2 *Dasiops*



3 *Dasiops*



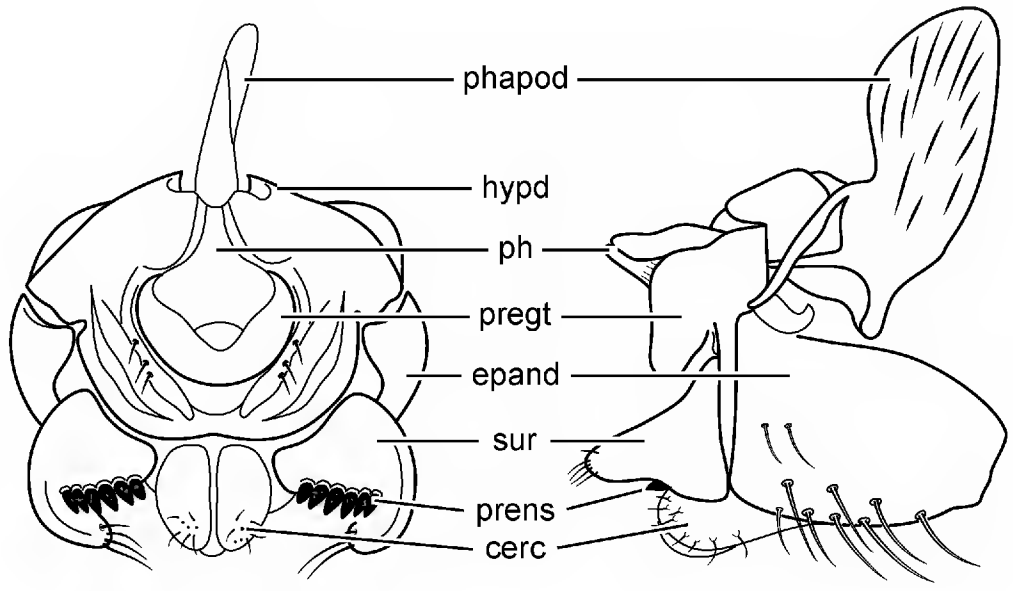
4 *Dasiops*

Figs 67.2–4. Head, thorax and wing of Lonchaeidae: (2) head of *Dasiops* sp., anterior view; (3) same, thorax and wing, lateral view; (4) same, wing, dorsal view. Figs 2–4 (after Morge 1963, figs 6, 2, 5, respectively).

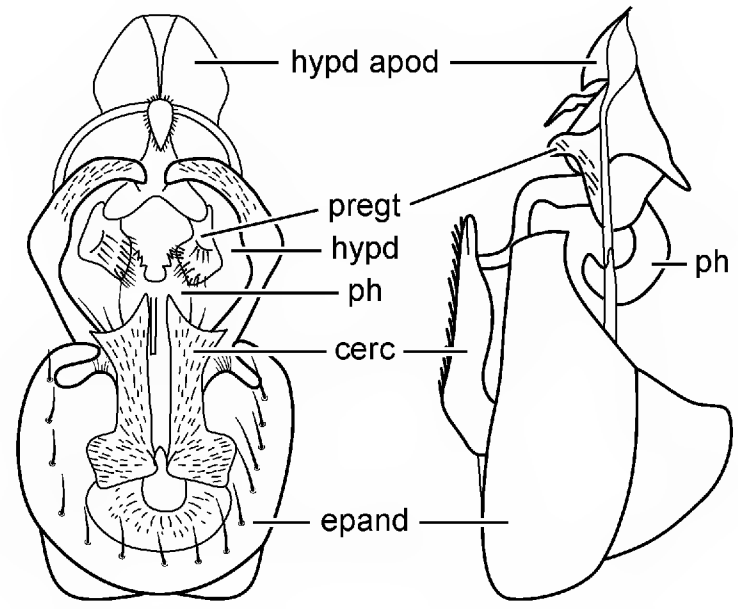
Abbreviations: al – alula; an lb – anal lobe; anepm – anepimeron; anepst – anepisternum; ar – arista; *bm* – basal medial cell; *C* – costal vein; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *dm* – discal medial cell; *dm–m* – discal medial crossvein; fc – face; gn – gena; i vt s – inner vertical seta; kepst – katepisternum; kepst s – katepisternal seta; lun – lunule; M_1 – first branch of media; M_4 – fourth branch of media; o vt s – outer vertical seta; pped – postpedicel; prepm – proepimeron; prepst – proepisternum; prth spr – prothoracic spiracle; pst s – poststigmatical seta; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; rc frorb s – reclinate fronto-orbital seta; *r–m* – radial–medial crossvein; *Sc* – subcostal vein; u calyp – upper calypter.

on the ventral side is a gap in each sheath, through which the apical part of the mouthhook protrudes. The integument on the ventral side is marked with arrangements of slight ridges, or cirri, leading towards the functional mouth, which lies between the two rectangular bases of the mouthhooks. The lobes ensheathing the mouthhooks are fused to varying degrees apically. For instance, they are separate in *Silba fumosa* (Egger, 1862) (non-Afrotropical) and fused in certain saproxylic *Lonchaea* species that feed on relatively dry, hard material where these features facilitate rasping and gathering. In contrast, separate lobes in *Silba* species, such as the Oriental *S. lashker* MacGowan & Razak, 2012, suit gathering oily food, such as that found in fruits or decaying plant stems. In most other lonchaeid larvae, the lobes differ from these two states, in being fused dorsally such that the oral cavity, the space between the lobes, is only open behind the mouthhooks. Such an arrangement enables a portion of liquid food to be isolated within the oral cavity each time the pseudocephalon is lowered into food.

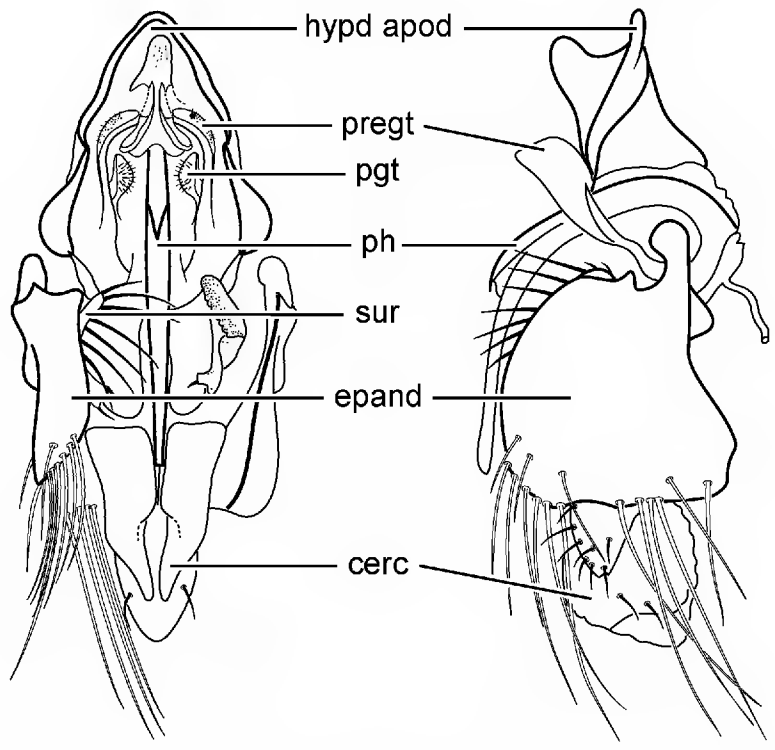
The larva of the gall-forming lonchaeid, *D. latifrons* (Meigen, 1826), a predominantly Mediterranean species, with close affinities to many Afrotropical *Dasiops*, demonstrates modifications of the cephaloskeleton for feeding on hard plant food within the gall (Fig. 19). The mouthhook is relatively large, with a short, blunt tip and a crescent-shaped base, due to a greatly extended projection of the anteroventral muscle attachment apodeme. Furthermore, the intermediate sclerite

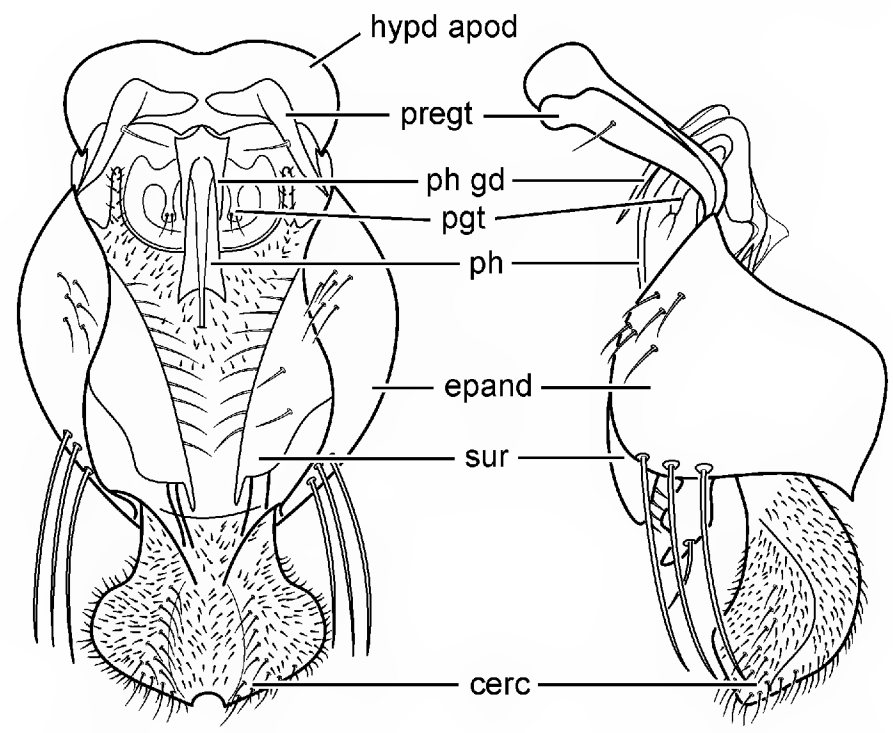


5 *Dasiops* ♂



6 *Dasiops* ♂ 7 *Fulgenta* ♂ 8 *Fulgenta* ♂





9 *Lamprolonchaea* ♂ 10 *Lamprolonchaea* ♂ 11 *Lonchaea* ♂ 12 *Lonchaea* ♂

Figs 67.5–12. Male terminalia of Lonchaeidae: (5) *Dasiops rugicavus* McAlpine, ventral view; (6) same, lateral view; (7) *Fulgenta saegeri* MacGowan, posterior view; (8) *F. excisa* MacGowan, lateral view; (9) *Lamprolonchaea smaradgi* (Walker), ventral view; (10) same, lateral view; (11) *Lonchaea grandiseta* MacGowan, ventral view; (12) same, lateral view. Figs 5, 6 (after McAlpine 1960, figs 25, 27), Figs 7, 8 (after MacGowan 2017, figs 4, 5), Figs 9, 10 (after Morge 1963, figs 70, 69, respectively).

Abbreviations: cerc – cercus; epand – epandrium; hypd – hypandrium; hypd apod – hypandrial apodeme; pgt – postgonite; ph – phallus; ph gd – phallic guide; phapod – phallapodeme; pregt – pregonite; prens – prensisetae; sur – surstylus.

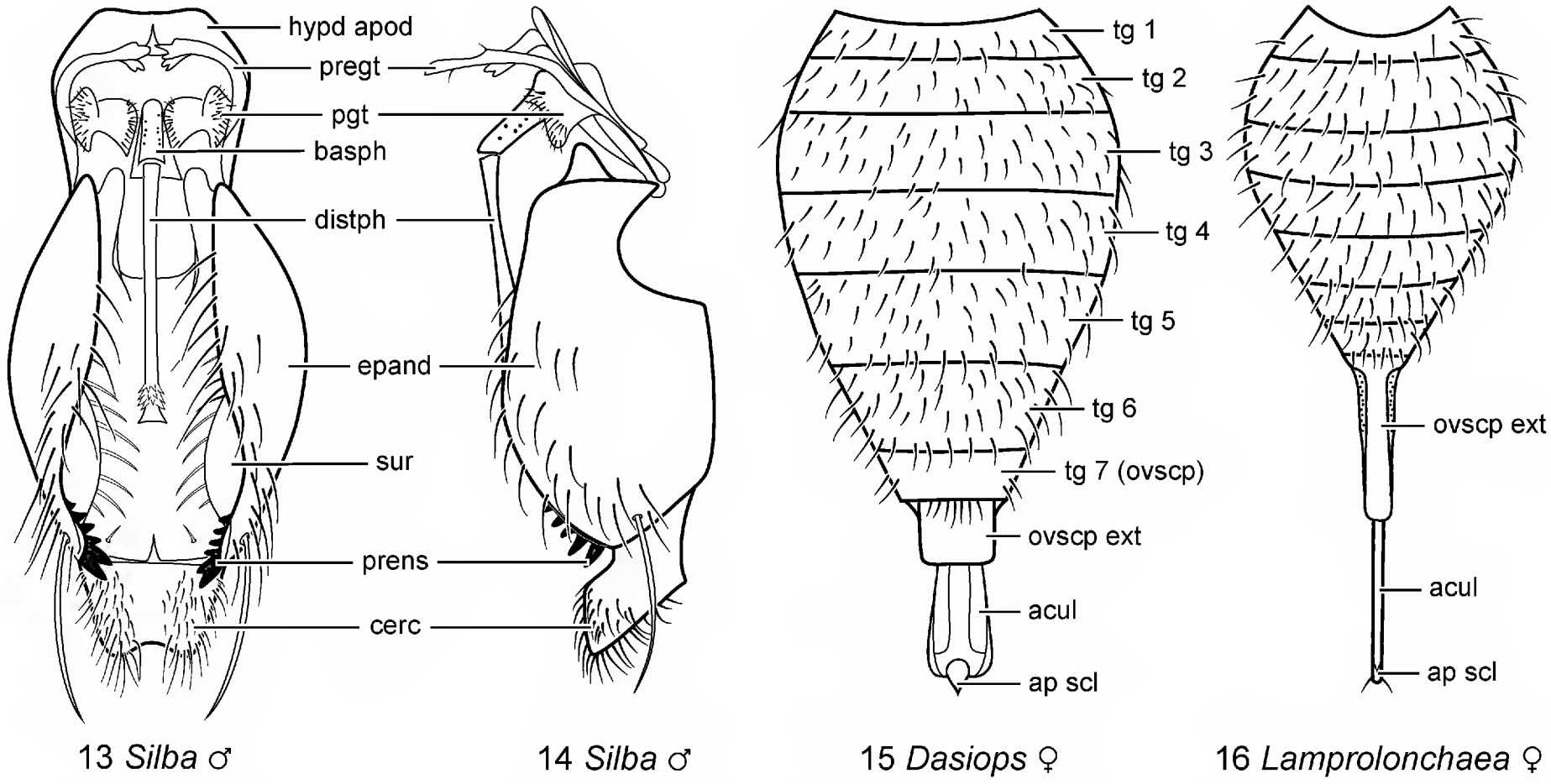
is short, deep and heavily sclerotised to support the mouthhook and the dental sclerite is relatively heavily sclerotised. The cephaloskeleton of *Dasiops latifrons* is also distinctive in lacking cibarial ridges.

The cephaloskeleton of *Lamprolonchaea smaragdi* (Walker, 1851) (Fig. 20), is very similar to *Silba lashker* (Fig. 21) and both are "typical", undifferentiated, indicative of a saprophagous lifestyle. Dental sclerites (Fig. 21) are present in *Silba* and *Lamprolonchaea*, but not differentiated in *D. latifrons*. *Lamprolonchaea smaradgi* and *S. lashker* also have cibarial ridges, indicating that they feed in a saprophagous manner.

One additional feature of the *D. latifrons* cephaloskeleton, not visible in *L. smaradgi* or *S. lashkeris*, is the development of paired accessory oral sclerites (Fig. 19). This development is associated with feeding on relatively solid food. In higher Cyclorrhapha, accessory oral sclerites are incorporated into the floor of the feeding channel and are not usually visible when the cephaloskeleton is viewed laterally, *e.g.*, *L. smaragdi*. However, when they are developed, as in *D. latifrons*, they appear in lateral view, as a narrow, curving bar that appears to connect the mouthhooks with the intermediate sclerite. They are not connected and are still part of the food channel and in a developed state, provide an extra support for the channel, which is probably necessary given the lumpy nature of the food. Developed accessory oral sclerites are present in most phytophages and in many saprophages feeding on similar, hard or lumpy food.

Unfortunately, we know relatively little of the detailed feeding mechanisms of Afrotropical lonchaeids or indeed of few other lonchaeids, aside from those mentioned above. Zoophagy has long been claimed for some lonchaeid larvae in the genus *Lonchaea*. It remains unclear, however, to what extent predation occurs in lonchaeid larvae. A detailed assessment of the evidence for and against predation *per se* can be found in Ferrar (1987: 208), who concluded that the subject was by no means closed.

Awadallah *et al*. (1980) undertook laboratory studies in Egypt on the biology of *Silba adipata* McAlpine, 1956 (misidentified as *S. virescens* Macquart, 1851). Egg hatch was highest at 25°C; the third-instar larval stage lasted 7.3 days at 30°C; the puparial stage lasted 33.4 days at 15°C and 21.3 days at 20°C. Adult eclosion was highest at 25°C and 75% relative humidity. The sex ratio was 1 : 1. Field observations indicated that there were six generations per year. No data exists for Afrotropical *Dasiops*, but Delgado *et al*. (2010) found development time from oviposition to eclosion of the adult of the Neotropical *D. saltans* (Townsend, 1913), averaging 20.8 days, with the mean duration of the egg stage 3.7 days, larval stage 9.05 days and puparial stage lasting eight days. On average, adults lived for approximately eight days. The only information for the genus *Lamprolonchaea* is for the Australasian species *L. brouniana* (Bezzi, 1919). Under laboratory conditions, the puparial stage of *L. brouniana* lasted for 11–14 days at 25°C; *mean* = 12 days (Blacket & Malipatil 2010).



Figs 67.13–16. Male terminalia and female abdomens of Lonchaeidae: (13) male terminalia of *Silba plumosissima* (Bezzi), ventral view; (14) same, lateral view; (15) female abdomen of *Dasiops anasillus* McAlpine, dorsal view (with distended terminalia); (16) same, *Lamprolonchaea smaragdi* (Walker). Fig. 15 (after Morge 1963, fig. 11).

Abbreviations: acul – aculeus; ap scl – apical sclerite; basph – basiphallus; cerc – cercus; distph – distiphallus; epand – epandrium; hypd apod – hypandrial apodeme; ovscp – oviscape; ovscp ext – oviscape extensions; pgt – postgonite; pregt – pregonite; prens – prensisetae; sur – surstylus; tg – tergite.

Economic significance

There have been few published accounts of economically important Lonchaeidae in the Afrotropical Region, aside from that of the Black fig fly, *Silba adipata* McAlpine, 1956, in South Africa (Giliomee *et al*. 2007) and of *Silba* species in Cameroon (Stephan *et al*. 2016). Other recorded instances of an association with commercial crops are mainly obtained from data labels appended to museum specimens, rather than from published records, or the concern of agriculturalists. This situation contrasts with that found in the Neotropics, where numerous species of the genus *Dasiops* and those in the genus *Neosilba* McAlpine, sister-group to *Silba*, are well-documented as having a substantial impact on commercial crops, such as Coffee, *Coffea* spp. (Rubiaceae) and Passion fruit, *Passiflora* spp. (Passifloraceae).

In the Afrotropical Region there are some data labels on *Lamprolonchaea* specimens which were reared from tomatoes and melons, but there are no published records of these as commercial pests. The best studied *Lamprolonchaea* species is the Australasian *L. brouniana*, which is considered as a serious agricultural pest, often the primary invader of tomatoes and other Solanaceae (capsicums and aubergines), Rosaceae (apricots, nectarines and peaches), Rutaceae (grapefruits, lemons, mandarins and oranges) and Lauraceae (avocados) (Blacket & Malipatil 2010). For *Lonchaea* species, McAlpine (1956, 1960) recorded *L. avida* McAlpine, 1960, as reared from squashes (*Cucurbita* spp.) and aubergine, *Solanum melongena* L. (Solanaceae) and *L. continentalis* Bezzi, 1920, from diseased pawpaw plants. The genus *Silba* is also associated with fruits, although whether species of the genus are primary or secondary invaders, is open to question. McAlpine (1956) noted that *S. ophyroides* (Bezzi, 1920) and *S. plumosissima* (Bezzi, 1919), were reared from ripening, or rotting tomatoes and *S. laevis* (Bezzi, 1920) from fruits of *Momordica involucrata* E.Mey (Cucurbitaceae). He also records *S. ophyroides* (as *S. fraterna* McAlpine, 1956) from ripening tomatoes, brinjal fruits (= aubergines) and fruits of *Solanum sodomeum* Hepper & P.-M.L.Jaeger (Solanaceae). McAlpine stated that H.K. Munro, the collector of the *S. ophyroides* specimens, noted that these were apparently a primary infestation of fruits by the lonchaeid larvae.

More recently Stephan *et al*. (2016) reported that a *Neosilba* species (almost certainly a misidentification of *Silba* species) caused losses of young fruits in two varieties of *Solanum aethiopicum* L. and one variety of *S. melongena* L. (Solanaceae) in the southern plateau and western highlands region of Cameroon. They regarded this *Silba* species as one of the main causes of fruit losses in these three varieties.

Given these records and the agricultural pest status of related Neotropical species, there appears to be a potential for Lonchaeidae to have an increasing economic impact in the Afrotropical Region, as agriculture intensifies.

Classification

Lonchaeidae are one of eight families included in the superfamily Tephritoidea. This superfamily comprises three monophyletic subgroups, one of which comprises the Lonchaeidae alone, considered as the earliest branching tephritoid lineage and sister-group to all other groups. This subgroup is distinguished by, among other things, unpatterned wings and mating in aerial swarms.

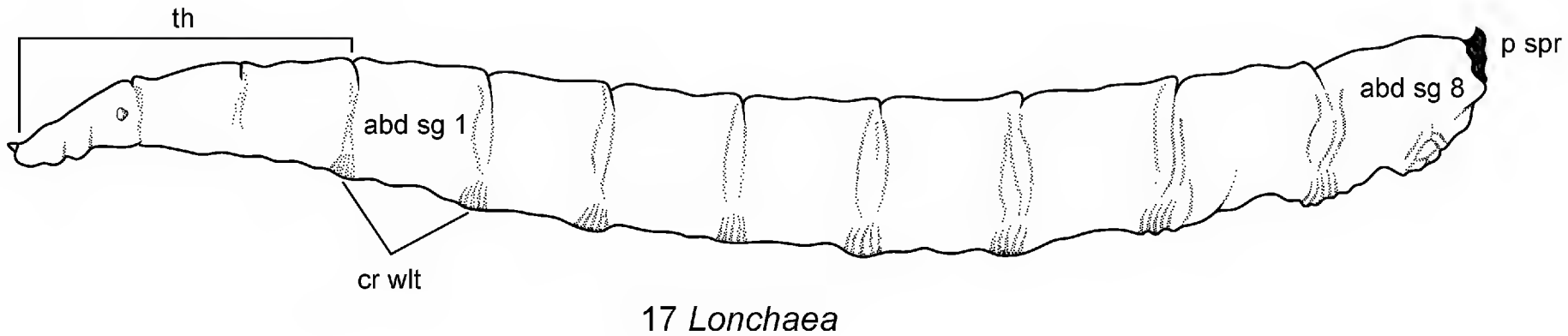
Korneyev (2000: 73) split the Tephritoidea into two sections, a monophyletic "higher Tephritoidea", comprising the Ulidiidae (= Otitidae and Pterocallidae (non-Afrotropical)), Platystomatidae, Pyrgotidae and Tephritidae and a paraphyletic "lower Tephritoidea", including the Lonchaeidae, Piophilidae, Pallopteridae (non-Afrotropical) and Richardiidae (non-Afrotropical). Morphological support is limited for the exact resolution of the relationships among the lower tephritoid families (Yeates *et al*. 2007). Historically the Pallopteridae was included within the Lonchaeidae, but due to differences in the structure of the male terminalia and larval ecology, it is now regarded as a distinct family.

Using DNA sequencing techniques, Han & Ro (2016) concluded that the Lonchaeidae was one of four families within the Piophilidae family-group, which also included non-Afrotropical Pallopteridae, Piophilidae and Eurygnathomyiidae. They recognised the Lonchaeidae and Pallopteridae as sister-groups. Their results also indicated that the three major lineages of the Piophilidae family-group (ancestral Eurygnathomyiidae, Piophilidae and Lonchaeidae, plus Pallopteridae) existed in the early part of the Eocene (*ca* 51 MYA).

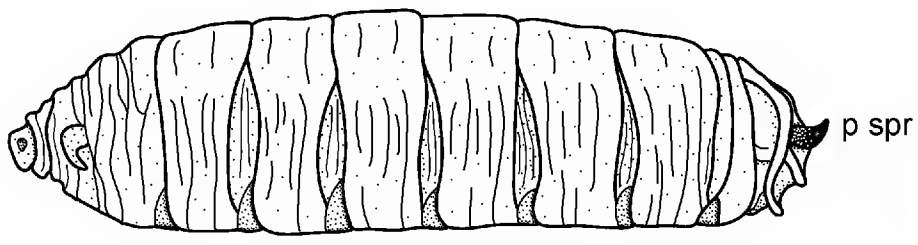
Identification

There are just over 570 species in nine genera of Lonchaeidae globally, five genera of which occur in the Afrotropical Region, with *Fulgenta* being endemic to it. The taxonomy and number of Afrotropical genera has remained relatively stable since McAlpine (1980: 630) listed 52 species in four genera. Recent unpublished work on the Afrotropical fauna undertaken in preparation of this chapter has identified *Earomyia*-like species which has cast into doubt the distinction between *Lamprolonchaea* and *Earomyia*. Further research is required to clarify the true taxonomic status of both genera and in the following identification key no distinction is made between them. The genus *Fulgenta* was erected in 2017 (MacGowan 2017).

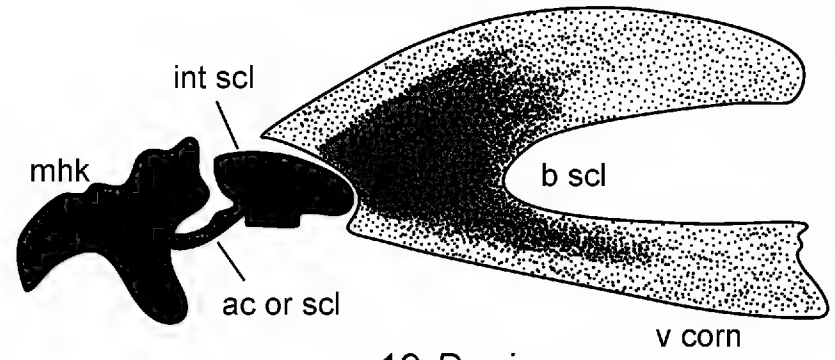
Currently, there are no published overviews, or comprehensive identification keys to Afrotropical Lonchaeidae. McAlpine (1960) reviewed the South African fauna and provided species-level identification keys to nine *Dasiops*, eight *Lonchaea* and eight *Silba* species. Morge (1980) treated the Lonchaeidae in sub-Saharan Africa and provided species-level identification keys to 11 *Dasiops* and three *Lamprolonchaea* species. MacGowan (2015) reviewed and provided an identification key to the *Silba admirabilis* species-group, which includes 15 Afrotropical species and MacGowan (2017) provided an identification key to the Afrotropical genus *Fulgenta*. An identification key to the seven genera occurring in Europe (excluding *Fulgenta*), was provided by MacGowan & Rotheray (2008). The most recent identification key to the lonchaeid genera of the world was provided by McAlpine (1987: 795) and this has subsequently been revised for the three genera within the tribe Lonchaeini by MacGowan & Okamoto (2013) and for those within the tribe Earomyinii by MacGowan (2017). Lonchaeidae are best micro-pinned in the field for later double-mounting (see Chapter 2), pinning through the thoracic dorsum is preferred as this does not damage any of the key features.



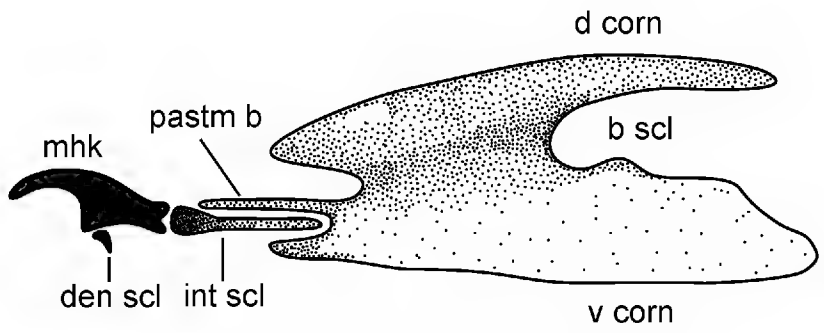
17 *Lonchaea*



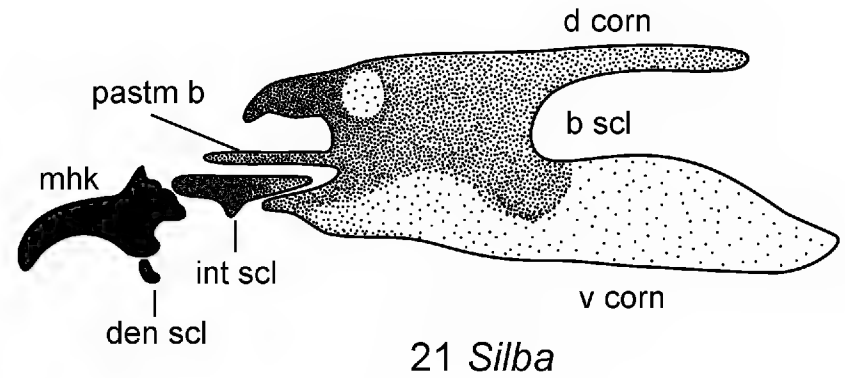
18 *Lonchaea*



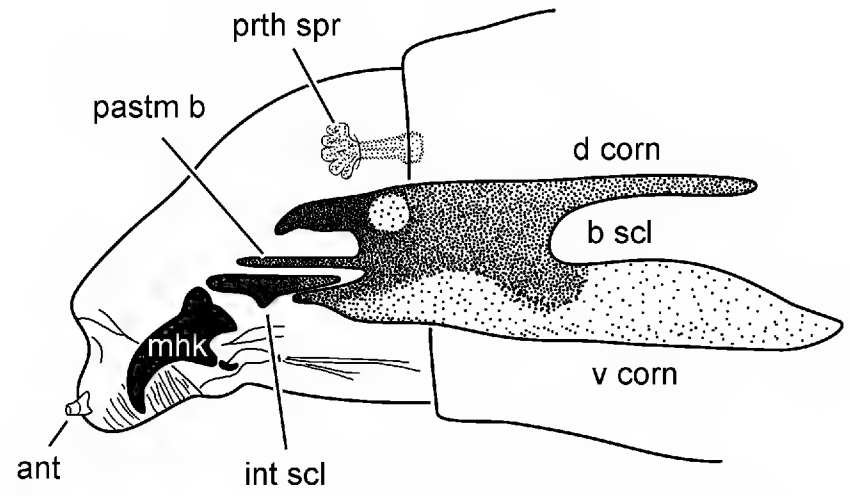
19 *Dasiops*



20 *Lamprolonchaea*



21 *Silba*



22 *Silba*

Figs 67.17–22. Immature stages of Lonchaeidae: (17) habitus of third-instar larva of *Lonchaea* sp., lateral view; (18) same, puparium; (19) larval cephaloskeleton of *Dasiops latifrons* (Meigen), lateral view (non-Afrotropical); (20) same, *Lamprolonchaea smaragdi* (Walker); (21) same, *Silba lashker* MacGowan & Razak (non-Afrotropical); (22) larval pseudocephalon, prothorax and metathorax of *S. lashker*, lateral view (indicating position of cephaloskeleton). Fig. 17 (after MacGowan & Rotheray 2008, fig. 10), Fig. 20 (after MacGowan *et al*. 2012, fig. 12).

Abbreviations: abd sg – abdominal segment; ac or scl – accessory oral sclerite; ant – antenna; b scl – basal sclerite; cr wlt – creeping welts; d corn – dorsal cornu; den scl – dental sclerite; int scl – intermediate sclerite; md – mandible; mhk – mouthhook; p spr – posterior spiracles; pastm b – parastomal bar; prth spr – prothoracic spiracles; th – thorax; v corn – ventral cornu.

Key to genera of Afrotropical Lonchaeidae

1. Thorax with poststigmatal setae/setulae on anterior marginal portion of anepisternum dorsal and slightly posterior to prothoracic spiracle (Fig. 3); male abdomen with 6 sternites (DASIOPINAE) . . . . . *Dasiops* Rondani
– Thorax without poststigmatal setae/setulae on anterior marginal portion of anepisternum; male abdomen with 5 sternites (LONCHAEINAE) 2
2. Head with lunule bare; body colour metallic or black; thorax with anepisternum with or without, strong anterior setae; katepisternum with single seta, or row of setae or setulae, close to dorsal margin (EAROMYIINI) 3
– Head with lunule setulose; body colour black; thorax with anepisternum with strong anterior setae; katepisternum with 1 or 2 strong setae close to dorsal margin (LONCHAEINI) 4
3. Male terminalia positioned within abdomen, with posterior surface usually posteriorly directed; epandrium without additional distinct sclerite, square to higher than deep, posterior margin often with strong setae; surstylus well-developed, with laminate lobes often extending beyond epandrium; cercus small, upright square or triangular, extending posteriorly from epandrium; phallus usually in form of a simple tube, without ornamentation (Figs 9, 10); body colour metallic green-blue to black; antennal arista usually bare . . . . . *Earomyia* Zetterstedt and *Lamprolonchaea* Bezzi
– Male terminalia with posterior surface ventrally directed; epandrium flattened, portion anterior to suture well-developed as distinct sclerite, posterior margin without strong setae; surstylus rudimentary, contained entirely within epandrium; cercus large, elongate, usually laminate; phallus often complex and ornamented (Figs 7, 8); body colour metallic blue-green; antennal arista pubescent to short plumose . . . . . *Fulgenta* MacGowan
4. Thorax with katepisternum usually with 1 strong seta; antennal arista bare or at most pubescent; surstylus of male terminalia without prensisetae, medial surface bearing setae or setulae, ventral margin often corrugated, extended or modified into spines or processes (Figs 11, 12) . . . . . *Lonchaea* Fallén
– Thorax with katepisternum usually with 2 strong setae; antennal arista usually plumose; surstylus of male terminalia with prensisetae, usually arranged in row, but sometimes individually, located either on medial surface at base of cercus or along ventral margin, otherwise inner surface usually virtually bare, ventral margin usually simple (Figs 13, 14) . . . . . *Silba* Macquart

Synopsis of the fauna

***Dasiops* Rondani** (Dasiopinae)**.** The subfamily Dasiopinae includes only this single genus, which is the second largest in the family, occurring in all zoogeographical regions, except Antarctica, with 128 described species. Seventeen species are recorded from the Afrotropical Region, but it is here estimated that there may be up to 100 undescribed species in the region. Afrotropical species have the body colour invariably blue-black to black; the antennal arista is always bare; the postpedicel is usually barely longer than wide; the gena is often with strong setae; the compound eye is bare or pilose; the basal tarsomeres are black or yellow; and the wing membrane is hyaline. Unlike other genera, species identification is often based on the shape of the female aculeus, which is often blade-like as an adaptation for piercing plant stems. The genus occurs throughout the Afrotropics, primarily associated with open savanna-type habitat. An identification key to the Southern African species was provided by McAlpine (1960). Morge (1980) described one additional species and updated the identification key of McAlpine (1960), covering the majority of the described fauna, although not all are keyed to species-level. No additional new Afrotropical *Dasiops* species have been described since Morge (1980).

***Earomyia* Zetterstedt** (Lonchaeinae: Earomyiini)**.** A genus of 23 described species recorded from the Nearctic and Palaearctic Regions. The genus was not previously recorded from the Afrotropical Region, but research undertaken in preparation of this chapter has resulted in the identification of several undescribed species. The separation of these Afrotropical species from *Lamprolonchaea* is, however, not clear-cut and a review of the relationship between both genera is required.

***Fulgenta* MacGowan** (Lonchaeinae: Earomyiini)**.** An endemic genus of 15 described species, but it is estimated here that up to 30 undescribed species may occur in the region. These are small, metallic green-blue flies, with a wing length of 2.5–3.1 mm; the antennal arista is pubescent to short plumose; the antennae are usually entirely black, but the postpedicel is occasionally slightly orange-brown on the medial base, with a length to depth ratio ranging from 1.5–2.0:1; the legs are black, with tarsomeres 1 and 2 pale and the apical tarsomeres darker; and the wing membrane is hyaline or occasionally with apical brown shading. The genus is distributed from South Africa north to Ethiopia and from Nigeria in the west to Kenya in the east. Based on the little information available, adults occur in habitats such as secondary woodland and lowland evergreen primary forest at elevations of up to 1,200 m. An identification key to all Afrotropical species was provided by MacGowan (2017).

***Lamprolonchaea* Bezzi** (Lonchaeinae: Earomyiini)**.** A genus of 17 described species, mainly occurring in the Afrotropical,

Australasian and Oriental Regions. Only one species, *L. smaradgi*, is currently recorded from the Afrotropics, but it is estimated here that up to 30 undescribed species (includes *Earomyia*; see above), may occur in the region. Afrotropical species have the body colour invariably shiny metallic blue-green; the antennal arista is plumose to bare; the postpedicel is 1–2 × longer than wide; the gena lacks strong setae; the compound eye is bare; the basal tarsomeres are almost always pale, seldom darkened; and the wing membrane is hyaline. *Lamprolonchaea smaradgi* occurs throughout the Afrotropics, associated with decaying fruits. An identification key to three Afrotropical species was provided by Morge (1980), but it is considered now as outdated, due to a redefinition of the genus by MacGowan (2017).

***Lonchaea* Fallén** (Lonchaeinae: Lonchaeini)**.** The largest genus in the family, occurring in all zoogeographical regions, except Antarctica, with 218 described species. Eighteen species are recorded from the Afrotropical Region, but it is estimated here that up to 100 undescribed species may occur in the region. Afrotropical species have the body colour invariably blue-black to black; the antennal arista is always bare; the postpedicel is 2–3 × longer than wide; the gena lacks strong setae; the compound eye is usually bare, but pilose in at least one sub-montane Afrotropical species; the basal tarsomeres are black or yellow; and the wing membrane is hyaline to slightly fumose. The genus occurs throughout the Afrotropics, in association with a wide range of grassland, scrub and forest habitat types. McAlpine (1960) reviewed the Southern African species, but later MacGowan (2005) added two new species.

***Silba* Macquart** (Lonchaeinae: Lonchaeini)**.** A genus of 112 described species, occurring primarily in the Afrotropical, Australasian and Oriental Regions, with a few species known from the Palaearctic and apparently one Neotropical. Thirty-four species are recorded from the Afrotropics, but it is estimated here that there may be up to 150 undescribed species in the region. Afrotropical species have the body colour invariably blue-black to black; the antennal arista almost always plumose, but bare in at least a few undescribed sub-montane Afrotropical species; the antennal postpedicel is *ca* 2.5–4 × longer than wide; the gena occasionally has strong setae; the compound eye is invariably bare; the tarsomeres are almost always black (except in the *S. admirabilis* McAlpine, 1956 species-group); and the wing membrane is hyaline, occasionally slightly yellowish or rarely fumose. *Silba* occurs throughout the Afrotropics, in association with a wide range of habitat types, although more frequently encountered in afforested habitats than other genera. McAlpine (1960) reviewed the Southern African species, but this work must be treated with caution, due to nomenclatural changes and a number of additional species have subsequently been described. Eight species were added by MacGowan (2005), one by MacGowan & Freidberg (2008) and thirteen by MacGowan (2015).

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PIOPHILIDAE 68

(Skipper Flies)

Burgert S. Muller

Fig. 68.1. Male of *Piophila casei* (L.) (Namibia) (photograph © S.A. Marshall).

Diagnosis

Moderately small-sized (body length: 3.0–6.0 mm), shiny black to dull brownish yellow acalyptrate flies (Fig. 1); body usually with strong black setae, relatively densely clothed in setulae; head with frons usually yellow in anterior ½ or more; wing membrane frequently glossy hyaline, with darker markings (some non-Afrotropical genera and species).

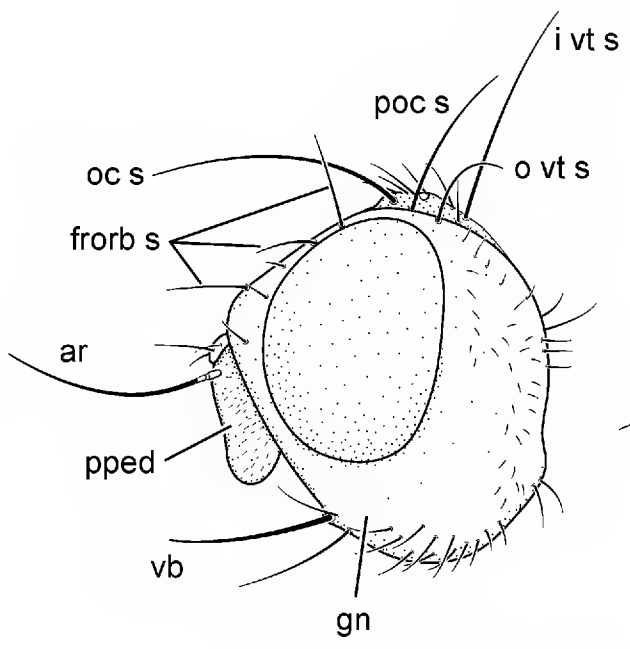
Head (Figs 2–6) scarcely as wide as thorax, higher than long (in lateral view), in all Afrotropical species; compound eye bare; frons setulose, *ca* as broad as long, equally so in both sexes, margins appearing virtually parallel, with anterior ½ or more usually weakly sclerotised, yellowish; ocellar triangle and orbital plates strongly sclerotised, frequently darker than remainder of frons (*Prochyliza ignifera* Martín-Vega, Ebejer & Whitmore, 2017, with frons, vertex and gena bright orange); mostly with 2, sometimes 1 pair of well-developed fronto-orbital setae, these occasionally absent; 1 pair of strongly antero-laterally directed ocellar setae; inner and outer vertical setae well-developed, subequal; postocellar setae divergent; vibrissa strongly differentiated, occasionally similar to surrounding setae; lunule bare; face concave in profile; antennal grooves somewhat recessed, membranous or at least weakly sclerotised along midline; clypeus relatively small; antenna short and porrect; scape short, simple; pedicel uniform in shape, without seam or projections on sides, although usually with conspicuous dorsal seta; postpedicel usually ovoid, rarely 2 × as long as wide; arista bare or pubescent, never plumose; proboscis short, labellum membranous; palpus usually relatively small.

Thorax with mesonotum varying between densely setulose and bare, usually shiny, but heavily pruinose in some non-Afrotropical genera; chaetotaxy: 0–2 pairs of postpronotal

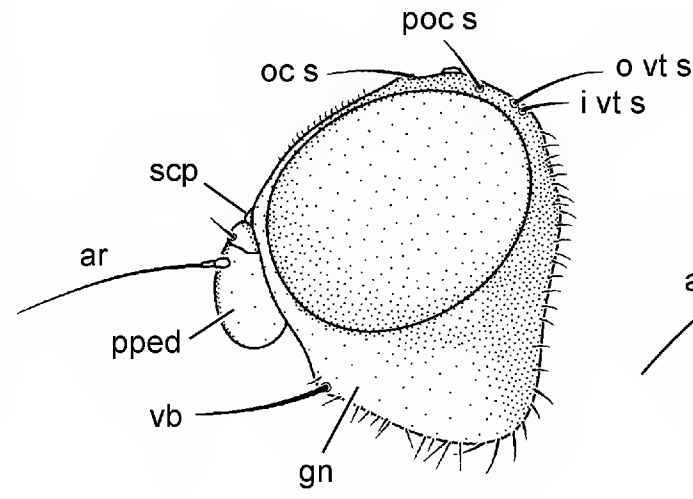
Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2021. Manual of Afrotropical Diptera. Volume 3. Brachycera—Cyclorrhapha, excluding Calyptratae. *Suricata* 8. South African National Biodiversity Institute, Pretoria; pp. 1597–1606.

setae, 1 pair supra-alar setae, 1 pair postalar setae, 0–1 pair presutural intra-alar setae, usually 1 pair postsutural intra-alar, 0–3 pairs presutural dorsocentral setae; 1–3 pairs postsutural dorsocentral setae, 0–1 pair postsutural acrostichal setae; pleura with anepisternum and anepimeron usually bare, although sometimes with 1 to several setae and numerous setulae (e.g., *Dasyphlebomyia* Becker); propleuron with proepisternal seta, disc of propleuron bare, without proepimeral seta; meron usually bare. Scutellum usually convex dorsally, with 4 marginal scutellar setae (Figs 8–10), rarely elongated, flattened dorsally, with > 4 marginal setae (e.g., *Dasyphlebomyia*, Fig. 7). Wing (Figs 11–15) relatively broad, with well-developed anal lobe and alula; membrane hyaline (patterned in non-Afrotropical genera: *Mycetaulus* Loew, *Neottiophilum* Frauenfeld, *Pseudoseps* Becker, *Thyreophora* Meigen), or largely brown fumose (*Dasyphlebomyia*); costal vein (*C*) broken just before subcostal vein (*Sc*), weakened (but never broken), immediately after humeral crossvein (*h*); all veins bare in Afrotropical genera; subcostal vein (*Sc*) complete, not connected to vein R_1; basal medial cell (*bm*) and discal medial cell (*dm*) usually separated by basal medial crossvein (*bm–m*); vein *CuA+CuP* traceable to wing margin, or rather abruptly discontinued. Legs (Fig. 1) relatively stout; femora and tibiae simple, latter without preapical dorsal seta, although frequently with other well-developed preapical ventral and lateral setae near apex; tarsi often quite setulose, with well-developed tarsal claws.

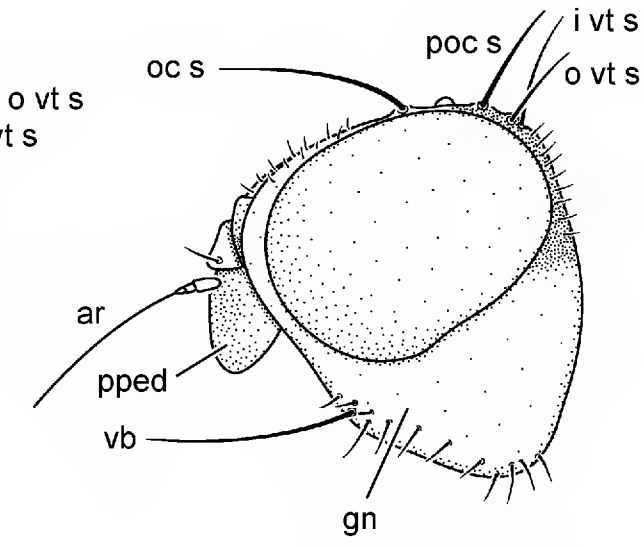
Abdomen with surface chaetotaxy varying from sparse and short, to densely setulose; surface appearing shiny black to dull brownish yellow; male abdomen (Fig. 16), typically asymmetrical; tergite 6 often mostly atrophied, partly fused with sternite 7, which is in part fused with sternite 8; male terminalia (Fig. 17), with surstyli in some cases greatly reduced, fused with epandrium (e.g., *Protopiophila* Duda); pre- and postgonites present; epiphallus variable in size, elaborated, usually spatulate; distiphallus usually long and flexible, looping rather than coiling, pubescent; phallapodeme fused with hypandrium; female terminalia (Fig. 18), with ovipositor telescopic, piercing; tergite and sternite 7 free, 2 strap-like rods arising from posterior margins, forming longitudinal struts in basal segment of ovipositor; tergite and sternite 8 forming shaft in form of 2 similar elongate straps in membrane; epiproct, hypoproct and



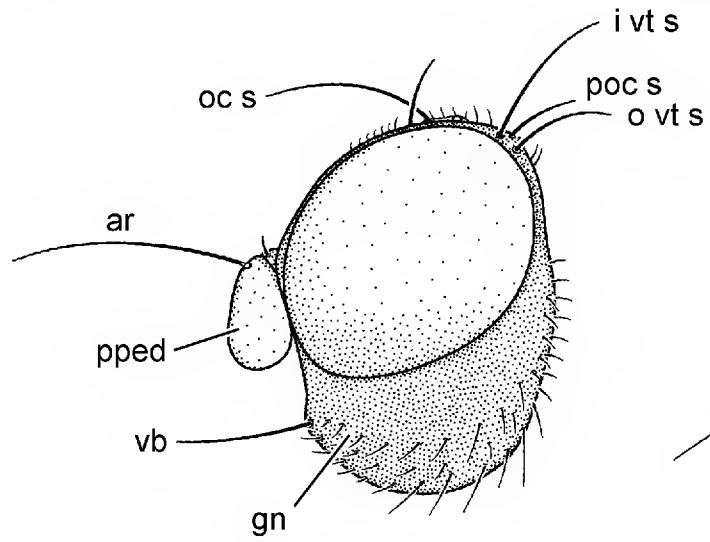
2 *Dasyphlebomyia*



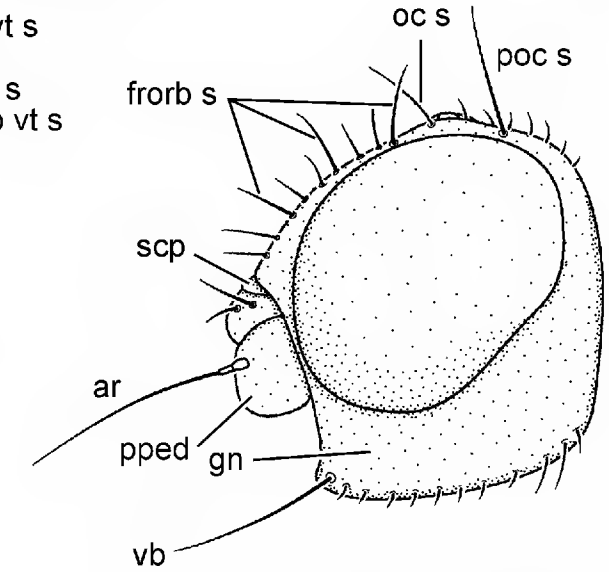
3 *Piophila*



4 *Prochyliza*



5 *Protopiophila*



6 *Pygopiophila*

Figs 68.2–6. Heads of Piophilidae (lateral views): (2) *Dasyphlebomyia stylata* Becker; (3) *Piophila casei* (L.); (4) *Prochyliza ignifera* Martín-Vega, Ebejer & Whitmore; (5) *Protopiophila aethiopica* Hennig; (6) *Pygopiophila sikorae* Duda.

Abbreviations: ar – arista; frorb s – fronto-orbital seta; gn – gena; i vt s – inner vertical seta; o vt s – outer vertical seta; oc s – ocellar seta; poc s – postocellar seta; pped – postpedicel; scp – scape; vb – vibrissa.

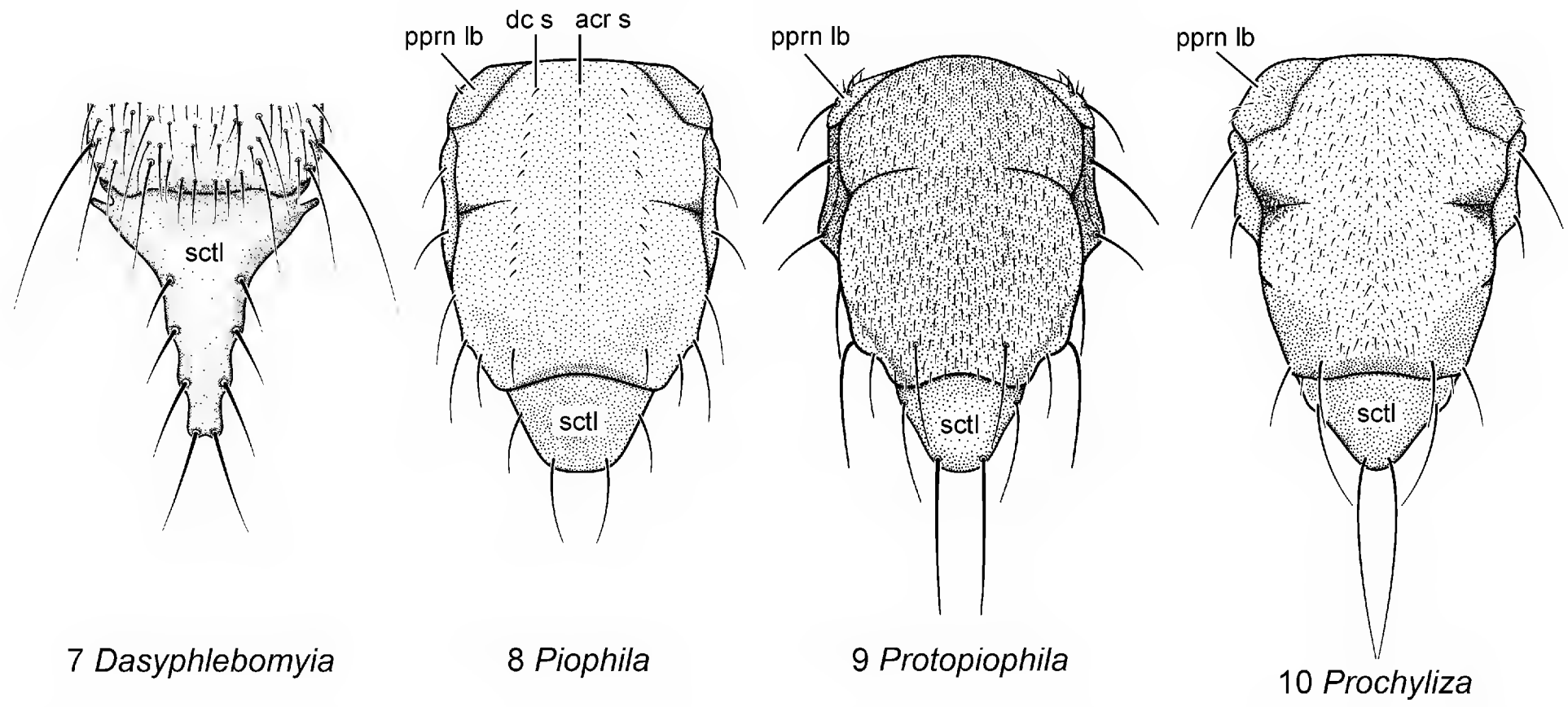
fused cerci forming tip of ovipositor; 2 spermathecae present, typically oval and sclerotised in Afrotropical genera, but *Piophila casei* (L., 1758) (erroneously considered by some authors to have 1 spermatheca (*i.e.*, Hardy & Delfinado 1980: 188; McAlpine 1977; Rochefort *et al* 2015), with 2 unsclerotised, largely reduced spermathecae (likely a derived state in Piophilidae (Kotrba 2019)).

Egg (Fig. 19), reticulated with chorionic sculpturing, fusiform, with nipple-like anterior micropore. Larva (Figs 20, 21) generally slender, cylindrical, tapered anteriorly, narrowed posteriorly, with truncated apex; segments with ventral creeping welts of spines, of which size and arrangement varies between species; posterior segments narrower than other abdominal segments, partially retractile, with at least 2 pairs of tubercles; cephaloskeleton (Fig. 24) with mouthhook slender, curved, pointed, without accessory tooth and dental sclerite; first-instar with cephaloskeleton clearly visible and weakly sclerotised; posterior spiracles present; dorsal and lateral spicules absent on all segments; ventral spicules (usually in rows of 3) on abdominal segments 2–8; terminal segment tapered posteriorly, without spines or setulae; posterior spiracles protruding, surrounded by 2 dorsal tubercles, 2 larger ventral tubercles and 3 pairs of lateral tubercles; second-instar with cephaloskeleton and posterior spiracles well-developed; prothoracic spiracle consisting of multiple papillae; posterior spiracle with 2 slit-like spiracular openings; third-instar up to 10 mm in length; cephaloskeleton robust, with strong mouthhook; prothoracic spiracle (Fig. 23), fan-shaped with 10 spiracular papillae arranged in 2 groups/lobes of five in *Piophila casei*, variable in other non-Afrotropical genera/species; posterior spiracle (Figs 21, 22), with 3 straight slit-like spiracular openings, arranged fan-like; spiracles situated on median sloping faces of spiracular prominences, appearing capable of being closed-off together. Puparium (Fig. 25), typically *ca* 5 mm in length, coppery red; cuticular features as in third-instar larva.

Adult Piophilidae are somewhat similar in general appearance to the families Sepsidae (see Chapter 79) and Agromyzidae (see Chapter 86). They can be readily distinguished from Sepsidae, in having well-developed palpi, hyaline wings and the abdomen not constricted basally and from Agromyzidae by the distinct subcostal vein, ending separate from vein R_1; females with fused cerci and lacking a hard tubular oviscape.

Biology and immature stages

Information on the mating behaviour of Afrotropical species is sparse, with only accounts for *Pi. casei* being available; these confined to description of copulation behaviour (Dufour 1844: 385; Swammerdam 1758: 721). One Palaearctic and two Nearctic species of genera occurring in the Afrotropics have, however, very interesting habits: males of *Centrophlebomyia furcata* (F.) run towards the female, and attempts to mount her such that their bodies are parallel to one another, with the female pressed down close to the substrate. If another male approaches then the "guarding" male will raise his mid legs in the direction of the approacher to ward him off. If the male is very small and all of his legs are preoccupied with holding on to the female, then the female may respond to mounting by raising her mid legs dorsomedially (Freidberg 1981). *Prochyliza xanthostoma* Walker, 1859, also known as "waltzing flies", have sparring bouts between males, with the two spreading their fore legs and holding on to each other's fore tarsi (much like



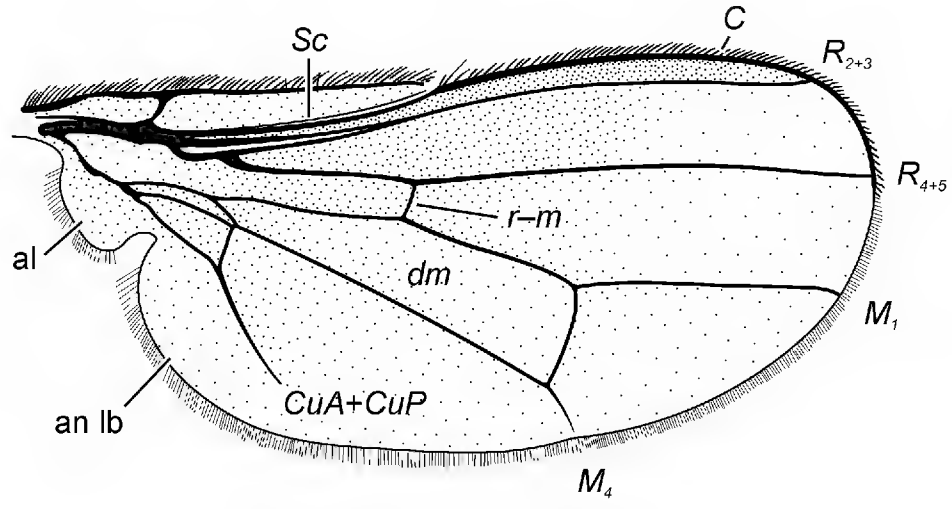
Figs 68.7–10. Thoraces and scutella of Piophilidae: (7) *Dasyphlebomyia stylata* Becker, dorsal view; (8) same, *Piophila casei* (L.); (9) same, *Protopiophila aethiopica* Hennig; (10) *Prochyliza ignifera* Martín-Vega, Ebejer & Whitmore. Fig. 7 (after McAlpine 1977, fig. 22).

Abbreviations: acr s – acrostichal setae; dc s – dorsocentral setae; pprn lb – postpronotal lobe; sctl – scutellum.

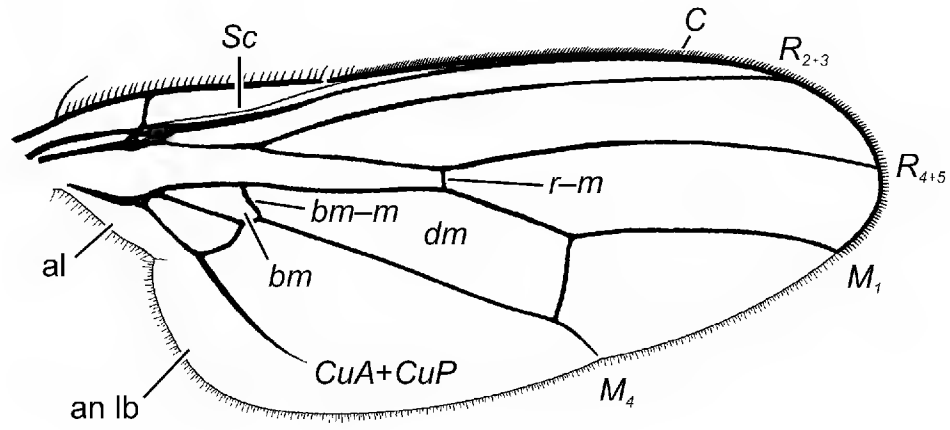
behaviour demonstrated by *Pi. casei*). Male courtship consists of a "zig-zag" dance, if the female reciprocates, mating takes place (Bonduriansky 2003). *Protopiophila litigata* Bonduriansky, 1995, also known as "antler flies" occur almost exclusively on discarded antlers of cervids and have very aggressive, territorial males. They typically spend their entire lives on one antler, and will spend much of their time defending oviposition sites. They also engage in mutual mate choice (Bonduriansky & Brooks 1998).

There is a marked difference in the breeding habits of subfamilies within the Piophilidae. Both tribes of the subfamily Piophilinae that occur in the Afrotropics, *i.e.*, Piophilini and Thyreophorini, are typically associated with and have been reared from carcasses in advanced stages of decomposition, bone marrow, dung and decaying organic matter. Several species are synanthropic and have become widespread, with *Pi. casei* (the Cheese skipper fly), being by far the most studied species of the family, due to its economic, forensic and medical significance. It is a pest of stored foodstuffs and animal products, and if ingested, can survive the action of mammalian digestive enzymes and cause serious intestinal scarification, before being evacuated alive (Hall & Smith 1993: 458). Larvae of the subfamily Neottiophilinae are by contrast ectoparasitic blood-feeders on nestling birds, although only the biology of *Neottiophilum praeustum* (Meigen, 1826) is known.

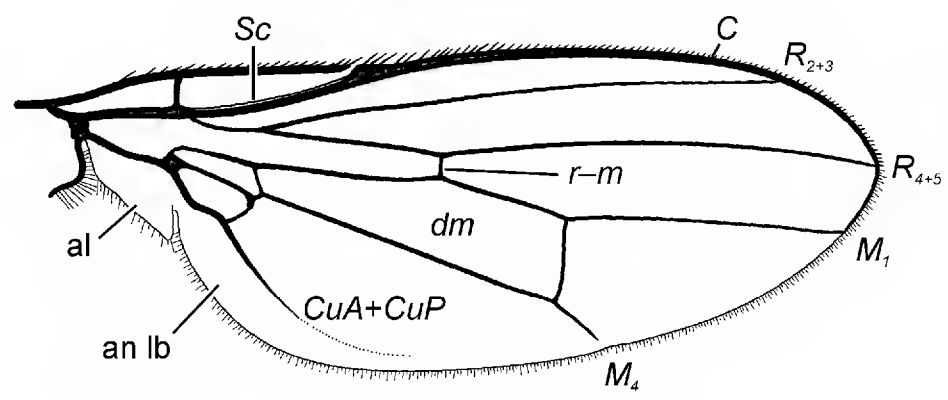
The third-instar larva of *Pi. casei* displays "skipping" behaviour, which is accomplished by bending the larval body and fastening the mouthhooks to a fold on the posterior end and



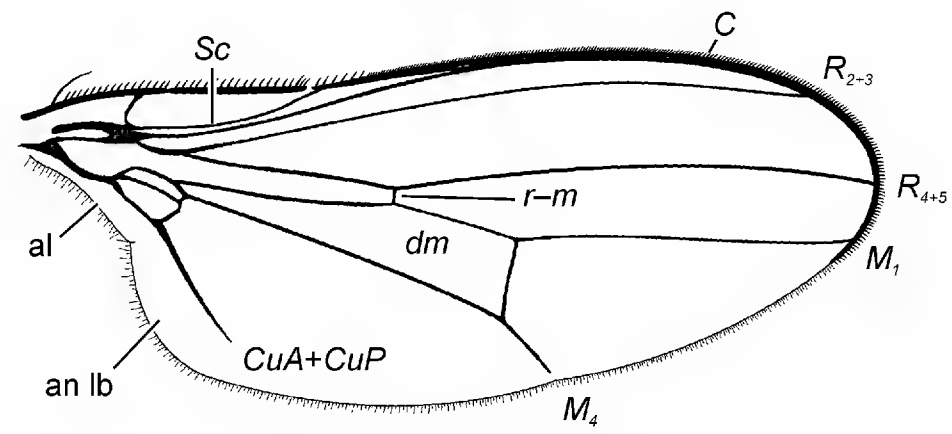
11 *Dasyphlebomyia*



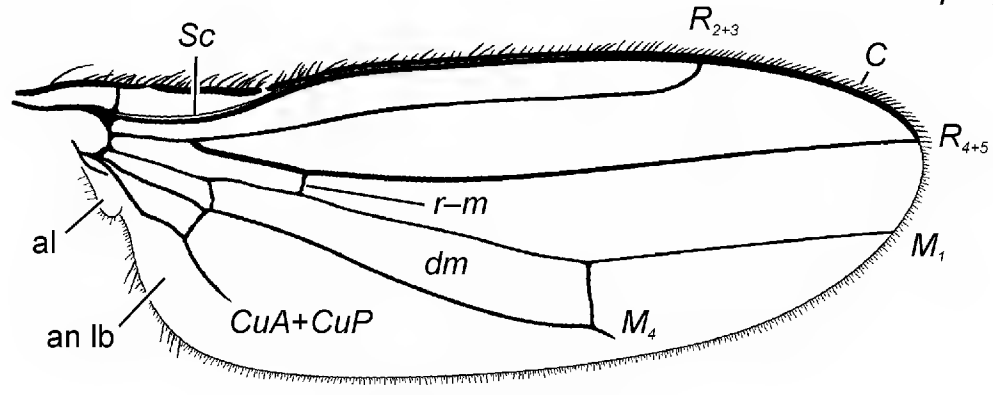
12 *Piophila*



13 *Prochyliza*



14 *Protopiophila*



15 *Pygopiophila*

Figs 68.11–15. Wings of Piophilidae (dorsal views): (11) *Dasyphlebomyia stylata* Becker; (12) *Piophila casei* (L.); (13) *Prochyliza ignifera* Martín-Vega, Ebejer & Whitmore; (14) *Protopiophila aethiopica* Hennig; (15) *Pygopiophila sikorae* Duda.

Abbreviations: al – alula; an lb – anal lobe; *bm* – basal medial cell; *bm–m* – basal medial crossvein; C – costal vein; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *dm* – discal medial cell; M_1 – first branch of media; M_4 – fourth branch of media; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Sc* – subcostal vein.

creating muscular tension in the body and releasing the hold, which results in a snapping action, that can propel the larva several inches at a time. This behaviour is not unique to *Pi. casei* and has been observed in other non-Afrotropical species as well as various other Tephritoidea and some other acalyptrate flies (Ferrar 1987: 40, 42, 148, 269, 298, 388).

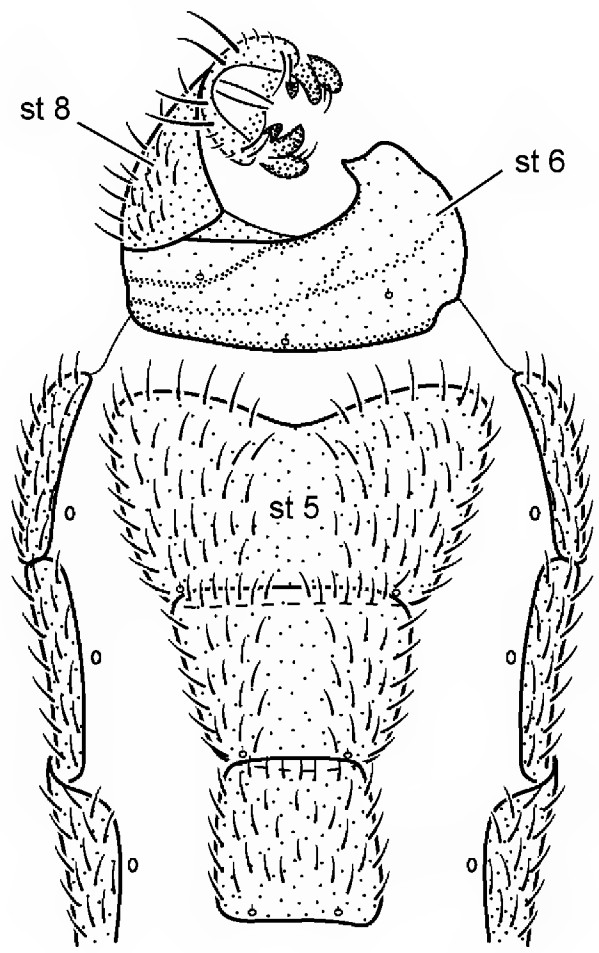
The morphology and biology of the immature stages of *Pi. casei* have been described in part by Candida & Agatino (2004), Ferrar (1987: 289), Greenberg (1971: 77), Hennig (1943: 26), Liu & Greenberg (1989), Martín-Vega *et al*. (2012), Oldroyd & Smith (1973: 304), Russo *et al*. (2006), Simmons (1927: 22), Smith (1986: 90), Sukontason *et al*. (2001) and Zumpt (1965: 24). Detailed descriptions of the immature stages of *Pi. megastigmata* McAlpine, 1978 have been made by Paños *et al*. (2013). The biology and immature stages of the monotypic genus *Dasyphlebomyia* as well as *Pygopiophila* Duda remain entirely unknown.

Economic significance

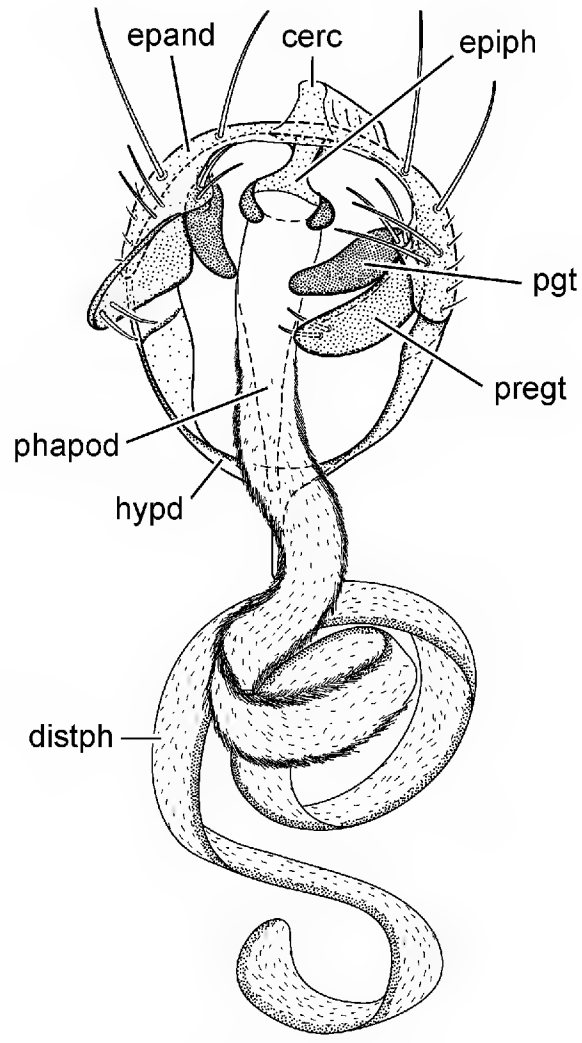
Several species of Piophilidae are known to occur on carrion or can be pests in food production (Zuska & Laštovka 1965). The most well-known is the virtually cosmopolitan *Pi. casei*, a strongly synanthropic fly, that has been a major problem in the food industry, especially where modern hygiene standards and refrigeration are lacking. Larvae develop in protein rich foods, such as cheese, other milk derivatives, ham and bacon, other cured meats and fish, in many cases undetected, due to larvae being positioned deep within the substrate (Busvine 1980: 228; Haines & Rees 1989: 25; Hall & Smith 1993: 458; Hegazi *et al*. 1978; Simmons (1927: 4), Zuska & Leštovska 1965).

Historically *Pi. casei* has formed an integral part in the production of the now outlawed Sardinian cheese, Casu marzu (meaning rotten/putrid cheese). Females oviposit in exposed pecorino cheese and larval feeding action promotes additional fermentation, breaking down fats and giving the cheese its unique texture and pungent taste (Overstreet 2003). Subsequent ingestion by humans of affected foods can lead to intestinal lesions (Ferrar 1987: 287). *Piophila casei* has also been reported in numerous cases of intestinal myiasis (as well as one case of nasal, one case of pulmonary and two cases of urogenital myiasis) (Francesconi & Lupi 2012; James 1947: 159, Simmons 1927: 7). Larvae can also attack animal hide and similar products, leading to further economic loss. Adults can also act as vectors for pathogens in food manufacturing industries (Greenberg 1971: 210).

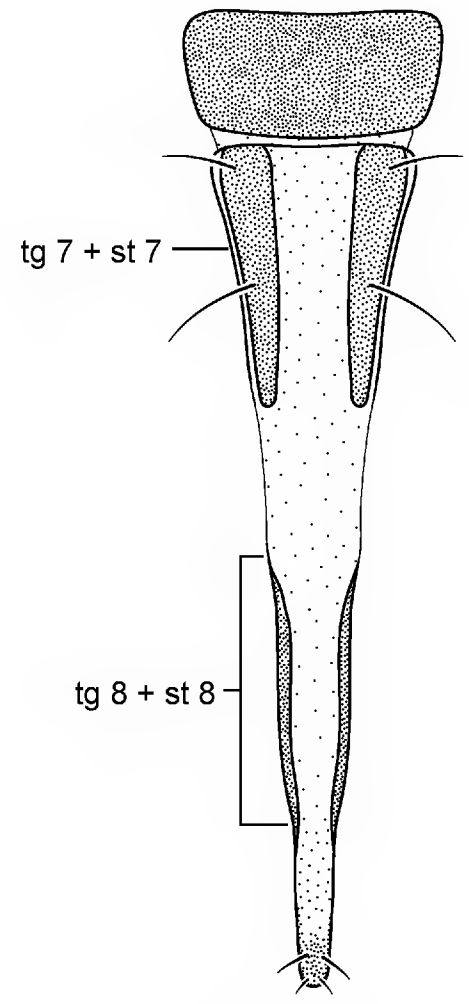
Several species of Piophilidae are of forensic and medicolegal importance (see Chapter 7), with *Pi. casei* and



16 *Piophila* ♂



17 *Piophila* ♂



18 *Protopiophila* ♀

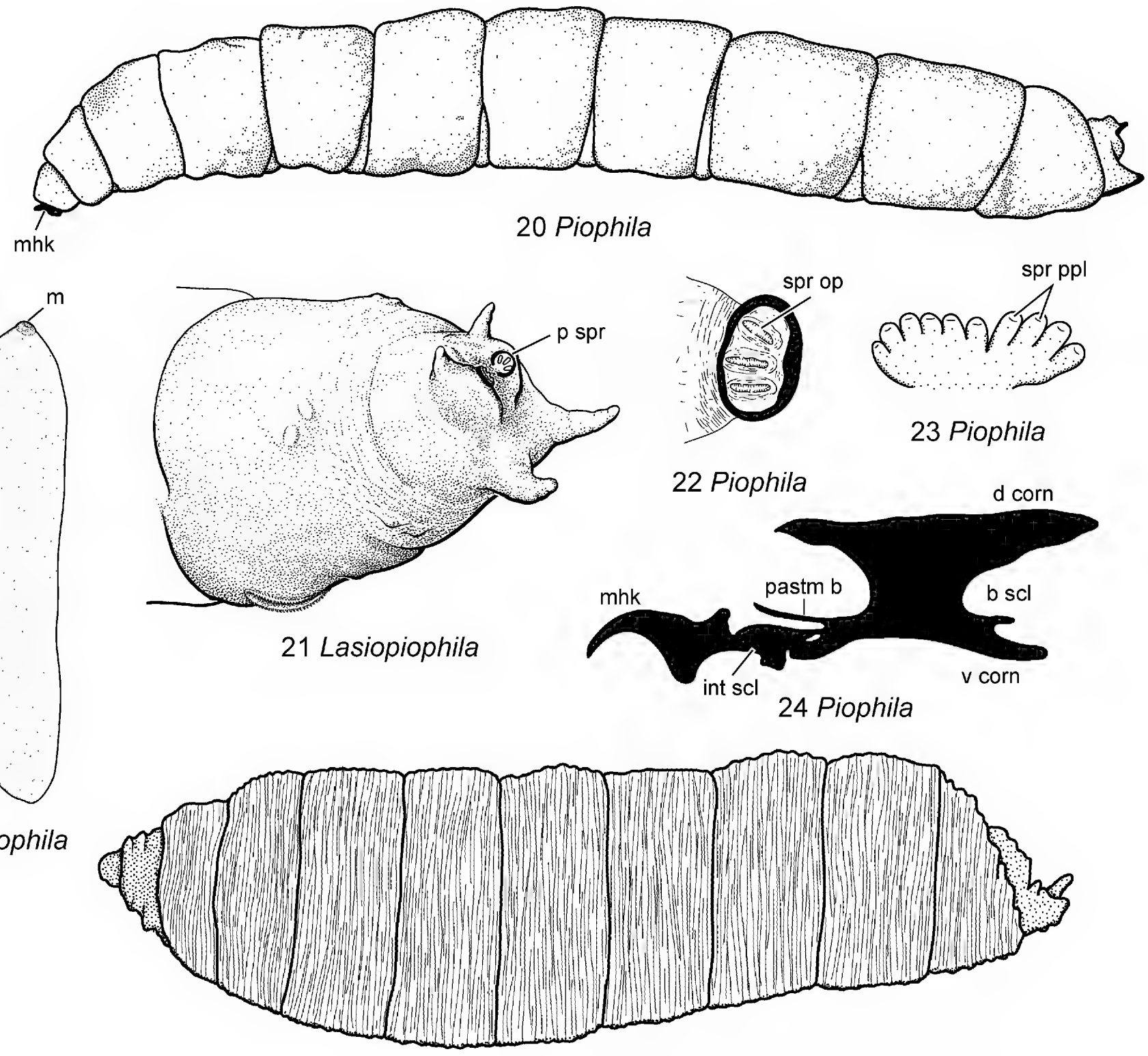
Figs 68.16–18. Abdomen and male and female terminalia of Piophilidae: (16) male abdomen of *Piophila casei* (L.), ventral view; (17) same, male terminalia; (18) female terminalia of *Protopiophila aethiopica* Hennig, ventral view. Fig. 16 (after McAlpine 1978, fig. 2).

Abbreviations: cerc – cercus; distph – distiphallus; epand – epandrium; epiph – epiphallus; hypd – hypandrium; pgt – postgonite; phapod – phallapodeme; pregt – pregonite; st – sternite; tg – tergite.

Pi. megastigmata, being the sole documented species in the Afrotropical forensic entomology literature (Braack 1986; Rochefort *et al*. 2015). *Piophila megastigmata* was also recorded for the first time on human corpses in Portugal (Prado e Castro *et al*. 2012). Some non-Afrotropical species of *Prochyliza* Walker and *Protopiophila* are also of forensic importance (Martín-Vega 2011). Piophilids are frequently cited in carrion succession studies globally, highlighting their involvement in decomposition. They are typically associated with carcasses in the advanced stages of decomposition, although adults may sometimes also be present at early stages, even if not ovipositing (Turchetto *et al*. 2001). A thorough review on the forensic importance of the family was provided by Martín-Vega (2011).

Classification

The Piophilidae are representatives of the superfamily Tephritoidea and have been considered to be most closely



Figs 68.19–25. Immature stages of Piophilidae: (19) egg of *Piophila casei* (L.), lateral view; (20) same, habitus of third-instar larva; (21) terminal segments of *Lasiopiophila pilosa* (Staeger), posterolateral view (non-Afrotropical); (22) posterior spiracle of third-instar larva of *Pi. casei*; (23) same, prothoracic spiracle; (24) same, cephaloskeleton of third-instar larva, lateral view; (25) puparial habitus of *Pi. megastigmata* McAlpine, lateral view. Fig. 19 (after Paños *et al*. 2013, fig. 1c), Figs 20, 22, 23 (after Ferrar 1987, figs 64.11, 64.27, 64.24, respectively), Fig. 21 (Teskey 1981, fig. 69), Fig. 24 (after Liu & Greenberg 1989, fig. 47), Fig. 25 (after Ebejer 2012, fig. 2).

Abbreviations: b scl – basal sclerite; d corn – dorsal cornu; int scl – intermediate sclerite; m – micropore; mhk – mouthhook; p spr – posterior spiracle; pastm b – parastomal bar; spr op – spiracular opening; spr ppl – spiracular papillae; v corn – ventral cornu.

related to the non-Afrotropical family Pallopteridae (Korneyev 2000: 10; McAlpine 1977, 1989: 1442), and although recent molecular phylogenetic analyses suggest that this may not be the case, it should be noted that at present any new relationships are poorly supported (e.g., Wiegmann *et al*. 2011).

Griffiths (1972) included Neottiophilidae and Thyreophoridae in his classification of Piophilidae and justified this move, based on the considerations provided by Hennig (1958, 1971) on the monophyly of Piophilidae *sensu lato* (Piophilariae *sensu* Hennig). Hennig also noted the close relationship of Neottiophilidae with that of Piophilidae and Thyreophoridae, noting that it was odd this had not been previously recognised and that they most probably form a separate group, even though a few of the morphological similarities, such head setation and wing venation are plesiomorphic (Hennig 1958: 604).

McAlpine (1977) further redefined Piophilidae to include the Neottiophilidae and Thyreophoridae into the two current subfamilies Neottiophilinae and Piophilinae, with the former including only the Neottiophilini and the latter the Mycetaulini, Piophilini and Thyreophorini.

Ozerov (2004) proposed an alternative classification, considering Neottiophilinae as a proper family, and synonymising *Liopiophila* Duda with *Prochyliza*, amongst others. This classification has, however, not been adopted very widely as it was not based on a phylogenetic analysis.

The higher classification adopted here follows that applied in the Nearctic and Palaearctic regional Diptera manuals (*i*.e., McAlpine 1987: 847; Ozerov 2000: 867), which includes the Neottiophilidae and Thyreophoridae in the Piophilidae, as previous authors had suggested.

Currently, there are 24 genera in two subfamilies: Neottiophilinae (2 genera; 4 species) and the Piophilinae, which consists of the three tribes: Mycetaulini (6 genera; 15 species), Piophilini (8; 41) and the Thyreophorini (6; 42) and one unplaced genus with one species. Only the tribes Piophilini and the Thyreophorini occur in the Afrotropical Region, together with the unplaced *Dasyphlebomyia* Becker.

Only one fossil species of Piophilidae is known: *Mycetaulus incretus* Melander, 1949 from the Oligocene Florissant fossil beds in Colorado, U.S.A. (Evenhuis 1994: 413).

Identification

McAlpine (1977) provided identification keys to most known world genera and species. McAlpine (1987: 851) and Ozerov (2000: 868) provided identification keys to Nearctic and Palaearctic genera, respectively. McAlpine (1989) provided an identification key to Australian species and Merz (1996) keyed the Swiss species. More recently, Rochefort *et al*. (2015) provided an identification key to the forensically important Piophilidae of the Nearctic Region. Piophilidae are best micro-pinned in the field for later double-mounting (see Chapter 2).

Key to genera of Afrotropical Piophilidae

1. Scutellum markedly elongate, flattened dorsally (Fig. 7) . . . . . *Dasyphlebomyia* Becker
– Scutellum normal, somewhat rounded, at least dorsally (e.g., Figs 8–10). 2
2. Wing with radial–medial crossvein (*r–m*) joining discal medial cell (*dm*) in basal ¼; vein R_{2+3} strongly arched at apex (Fig. 15) . . . . . *Pygopiophila* Duda
– Wing with radial–medial crossvein (*r–m*) joining discal medial cell (*dm*) at or beyond middle; vein R_{2+3} relatively straight at apex (e.g., Figs 11–14). 3
3. Thorax with postpronotal lobe with 2 setae, the inner one inclinate (Fig. 9) . . . . . *Protopiophila* Duda
– Thorax with postpronotal lobe without setae, sometimes with scattered setulae 4
4. Thorax with scutum mostly bare, setulae largely confined to 3 isolated rows in acrostichal and dorsocentral fields (Fig. 8). . . . . *Piophila* Fallén
– Thorax with scutum uniformly setulose, setulae not in isolated rows (Fig. 10) . . . . . *Prochyliza* Walker

Synopsis of the fauna

A small, but virtually cosmopolitan family of 82 described species, with greatest species diversity in the temperate and boreal parts of the Holarctic Realm (Ozerov & Norrbom 2010: 868; Pape *et al*. 2009: 443). Only seven species in five genera are recorded from the Afrotropical Region.

***Dasyphlebomyia* Becker** (Piophilinae: Piophilini: Thyreophorina)**.** An endemic monotypic genus, with the single described species, *D. stylata* Becker, 1914, described from Mt Kilimanjaro, Tanzania (as Kenya) and later recorded from Misingi and Maranga in Tanzania (McAlpine 1977). Steyskal (1973) included the genus in an identification key to genera of "Thyreophoridae" and figured the male scutellum. The biology and immature stages remain unknown. See Fig. 2 for an example of the head of the genus and Fig. 11 for the wing. The genus was also keyed by McAlpine (1977), who provided a diagnosis of the genus that should facilitate identification.

***Piophila* Fallén** (Piophilinae: Piophilini: Piophilina)**.** A genus of two described species globally. One species, *Pi. megastigmata*, was omitted from the Afrotropical Catalogue by Cogan (1980: 633). The species was historically regarded as endemic to South Africa (Kruger National Park, associated with Impala carcasses), but was subsequently recorded from

Spain by Martín-Vega *et al*. (2011), as well as Algeria by Saifi *et al*. (2016). The second species is the virtually cosmopolitan Cheese skipper, *Pi. casei*, thought to be primarily Holarctic (McAlpine 1978; Zumpt 1965: 24). This species is associated with humans globally, as a common pest of proteinaceous animal products (McAlpine 1978) and is also found in association with carcasses in the wild, usually at the final stages of decomposition (Cogan 1980: 633). The species is also important in forensic entomology (see "Economic significance" section above). The two described species occur sympatrically, with *Pi. megastigmata* being more abundant than *Pi. casei* in autumn, with the opposite being the case in spring (Martín-Vega *et al*. 2011). The immature stages of *Pi. casei* are discussed in more detail above. See Fig. 3 for an example of the head of the genus, Fig. 12 for the wing and Figs 16 and 17 for the male terminalia. An identification key to the two species of the genus was provided by McAlpine (1978).

Protopiophila **Duda** (Piophilinae: Piophilini: Piophilina)**.** A genus of 11 described species, occurring in all zoogeographical regions, except Antarctica. Two endemic species are recorded from the Afrotropical Region, *Pr. aethiopica* Hennig, 1951, from South Africa and *Pr. leucodactyla* Hennig, 1954, from Tanzania. The genus was revised by Harrison (1960*a*, *b*). Cogan (1980: 633) treated *Protopiophila* as a subgenus of *Piophila*. The immature stages are not well-studied, with Bonduriansky (1995) only providing measurements for a species described from the Nearctic, with limited behavioural notes. See Fig. 5 for an example of the head of the genus and Fig. 14 for the wing. An identification key to most species (including the two Afrotropical species), was provided by McAlpine (1977), which was amended by Bonduriansky (1995).

Prochyliza **Walker** (Piophilinae: Piophilini: Piophilina)**.** A genus of nine described species occurring in the Afrotropical, Nearctic, Neotropical and Palaearctic Regions. One species, *Pro. ignifera*, occurs in the Afrotropics, described from the Indian Ocean islands of Aldabra Is. and Réunion Is. (Martín-Vega *et al*. 2017). As with other Piophilidae the species is sarcosaprophagous. The immature stages of *Pro. nigrimana* (Meigen, 1826) (a non-Afrotropical species that also develops on carrion and in food products), were described in detail by Martín-Vega *et al*. (2012) and compared to those of *Piophila casei*. See Fig. 4 for an example of the head of the genus and Fig. 13 for the wing. The genus was treated by McAlpine (1977) and more recently by Martín-Vega (2014), who also provided an identification key to all species, excluding *Pro. ignifera*. Martín-Vega *et al*. (2017) later provided an amended key to species, which includes *Pro. ignifera*.

Pygopiophila **Duda** (Unassigned). An endemic monotypic genus, with the single described species, *Py. sikorae* Duda, 1927, only known from the unique holotype from Madagascar. McAlpine (1977) provided an English translation of Duda's original German description, which should facilitate identification, but did not examine the type specimen and only tentatively placed the genus in the subfamily Piophilinae. Cogan (1980: 634) listed *Pygopiophila* as "Unplaced genus of Piophilidae". The type material is in need of re-examination and the biology and immature stages remain unknown. See Fig. 6 for an example of the head of the genus and Fig. 15 for the wing.

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ULIDIIDAE 69

(Picture-winged Flies)

Elena P. Kameneva and David A. Barraclough

Fig. 69.1. Female of *Physiphora clausa* (Macquart) (Malaysia) (photograph © A. Kei C. Wong).

Diagnosis

Medium-sized (body length: 2–14 mm; Afrotropical species usually 4–7 mm) acalyptrate flies with moderately elongate body (Fig. 1); colouration yellow to brown or black, with pattern of microtrichose maculae or fasciae, often with metallic blue or green sheen.

Head (Figs 2–13) variously shaped; inner and outer vertical setae and ocellar setae divergent (Fig. 5); postocellar and orbital (1 or 2, anterior shortest) setae present (Fig. 5); frontal setae absent in Afrotropical species; frons sometimes pitted or rugose (Fig. 4); clypeus moderately large, occasionally very large (Fig. 3); proboscis with moderately large prementum (Fig. 2).

Thorax longer than wide (Figs 14–16), rarely almost as long as wide (Fig. 17). Wing membrane (Figs 21–30) with pattern of dark maculae or fasciae, in Afrotropical species often entirely hyaline; subcostal vein (*Sc*) complete; costal vein (*C*) with distinct humeral break, subcostal break indistinct (Fig. 21). Legs in males of *Physiphora* Fallén with fore femur often with thickened setae (Fig. 20); tibiae without dorsal setae or setulae (Fig. 20).

Abdomen from shiny in *Physiphora* and *Acrosticta* Loew to entirely microtrichose in *Melieria* Robineau-Desvoidy; male terminalia with phallus long, concealed in membranous pocket on ventral side of abdomen, often bearing spines in Otitinae (Fig. 36), or glans-like structure at apex and 1–3 membranous projections or caecum (plural caeca), in most Ulidiinae: Ulidiini (Figs 34, 35); epandrium (Figs 31, 32, 37, 38) in Afrotropical taxa oval; surstylus usually short and partly separated from epandrium (Fig. 31); subepandrial sclerite (or bacilliform sclerite), commonly V-shaped, setulose (Fig. 32), often forming

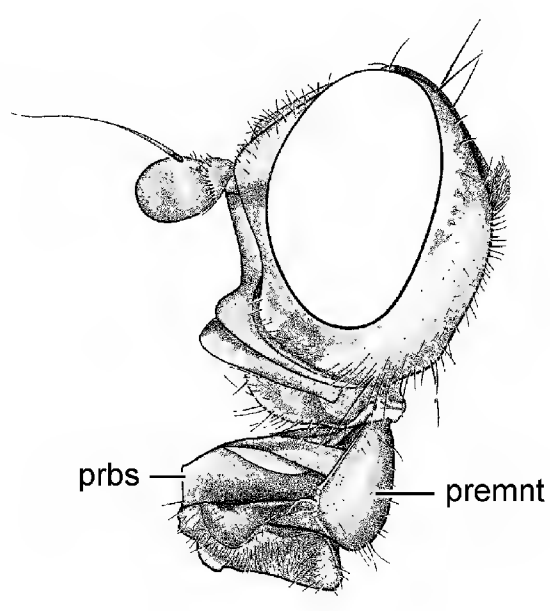
Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2021. Manual of Afrotropical Diptera. Volume 3. Brachycera—Cyclorrhapha, excluding Calyptratae. *Suricata* 8. South African National Biodiversity Institute, Pretoria; pp. 1607–1618.

posteroventral lobe (inner surstylus) with thickened setae (prensisetae); in Afrotropical *Arborotites* Barraclough and *Namibotites* Barraclough, each with 2–3 prensisetae (3–30 in Holarctic genera); female abdomen as in other Tephritoidea, with telescopic ovipositor (Fig. 39); sternites 4–6 with long, narrow medioventral apodemes in Myennidini and Otitini (Fig. 40) or without in Lipsanini and Ulidiini (Fig. 39); eversible membrane with long taeniae; tergosternite 8 usually narrow and stiff, bearing longitudinal rows of mechanoreceptory sensilla (Fig. 45); cercal unit in Afrotropical species oval or triangular, bearing sets of long and short setulae (Figs 41, 42, 45) and also campaniform sensilla; anal opening (slit) on dorsal surface of cercal unit.

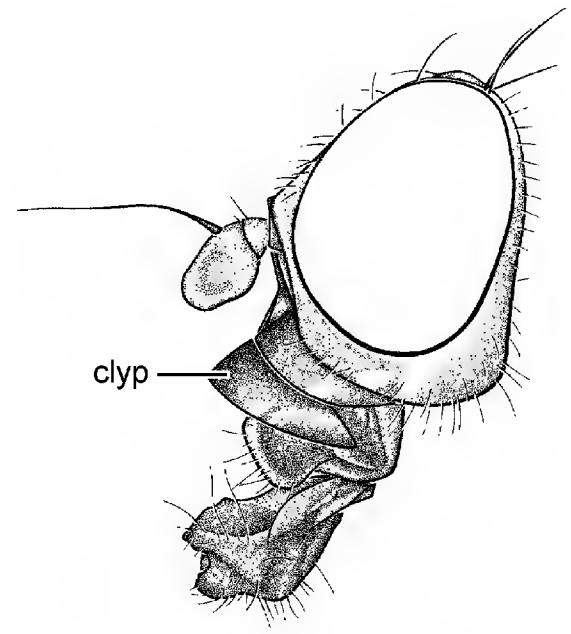
Ulidiidae differ from Tephritidae (see Chapter 71), by the complete subcostal vein (*Sc*) and lack of anepimeral setae. Platystomatidae (see Chapter 70) have cell *cua* closed with an arcuate or straight crossvein, whereas in Ulidiidae this crossvein is sinuate, forming an acutely produced, often very long, posteroapical lobe; platystomatids also have distinctive anepimeral setae. Unlike Afrotropical Pyrgotidae (see Chapter 72), all Ulidiidae have ocelli. Males of Platystomatidae, Pyrgotidae and Tephritidae have the phallus coiled in a special membranous "pocket" on the dorsal side of the abdomen at rest, whereas ulidiids have this on the ventral side. As with other tephritoids, ulidiids never have rows of strong setae on the dorsum of the tibiae, distinguishing them also from Lauxaniidae (see Chapter 74) and Sciomyzidae (see Chapter 78).

Biology and immature stages

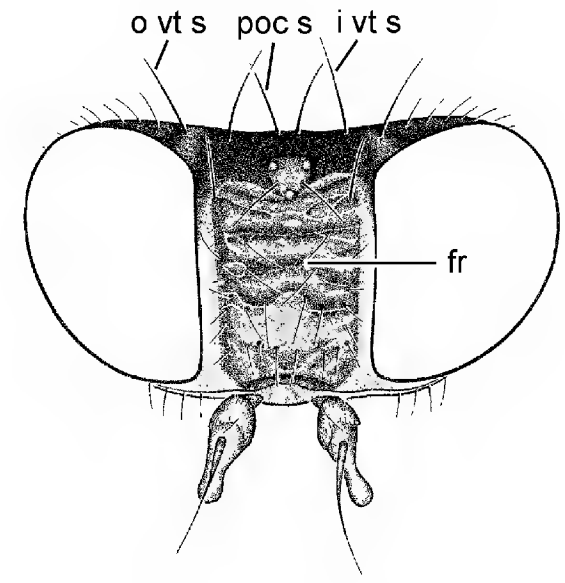
Larvae of most Ulidiidae are saprophagous, but virtually nothing is known regarding the biology of Afrotropical species. Larvae of the Holarctic genera *Myennis* Robineau-Desvoidy and *Pseudotephritis* Johnson (Otitinae: Myennidini), as well as some Seiopterini and Ulidiini, occur beneath the bark of fallen



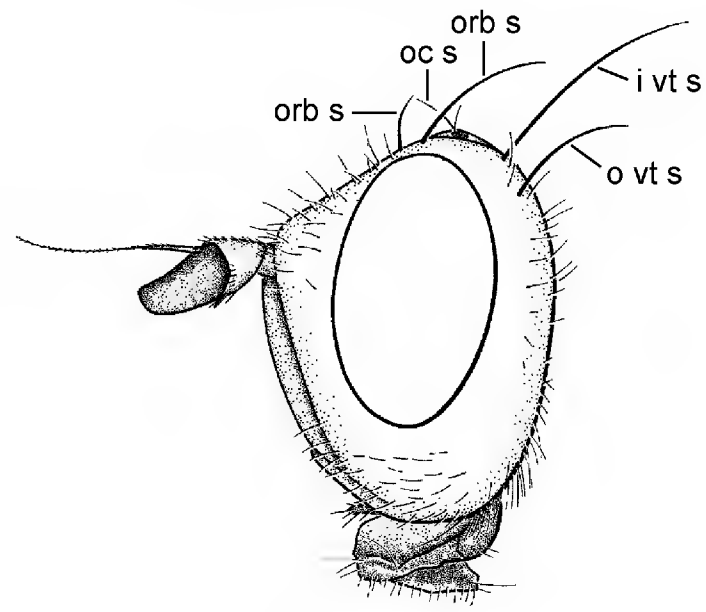
2 *Arborotites*



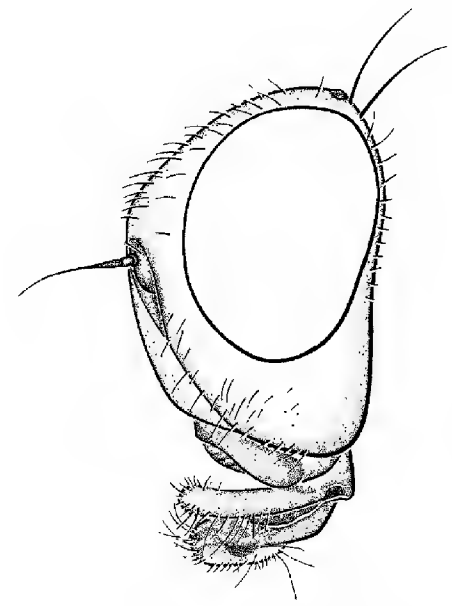
3 *Acrosticta*



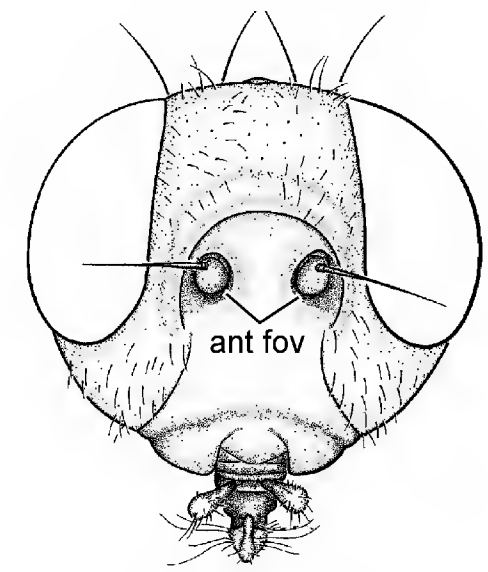
4 *Acrosticta*



5 *Melieria*



6 *Namibotites*



7 *Namibotites*

Figs 69.2–7. Heads of Ulidiidae: (2) *Arborotites stuckenbergi* Barraclough, lateral view; (3) *Acrosticta apicalis* (Williston), lateral view; (4) same, dorsal view; (5) *Melieria nigritarsis* Becker, lateral view; (6) *Namibotites argentata* Barraclough, lateral view; (7) same, anterior view. Figs 2–7 (Barraclough 2000, figs 3, 1, 2, 5–7, respectively).

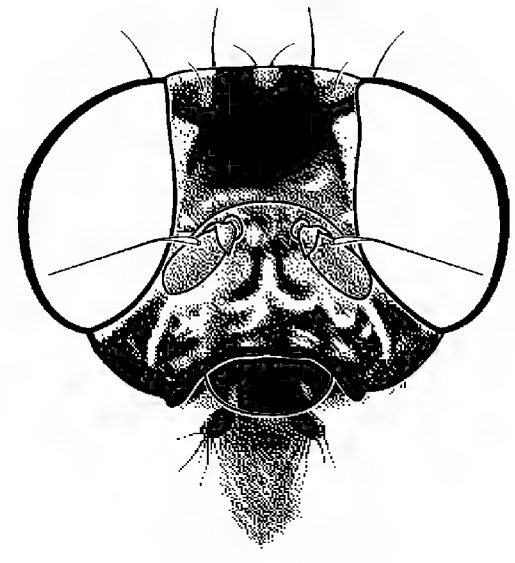
Abbreviations: ant fov – antennal foveae; clyp – clypeus; fr – frons; i vt s – inner vertical seta; o vt s – outer vertical seta; oc s – ocellar seta; orb s – orbital seta; poc s – postocellar seta; prbs – proboscis; premnt – prementum.

trees (Krivosheina & Kovalev 1972; Krivosheina & Krivosheina 1997*a*, *b*, *c*; Lukasheva 1987: 52); larvae of the Afrotropical genera *Acatochaeta* Enderlein and *Arborotites*, related to *Myennis* and *Pseudotephritis*, are believed to have similar habits.

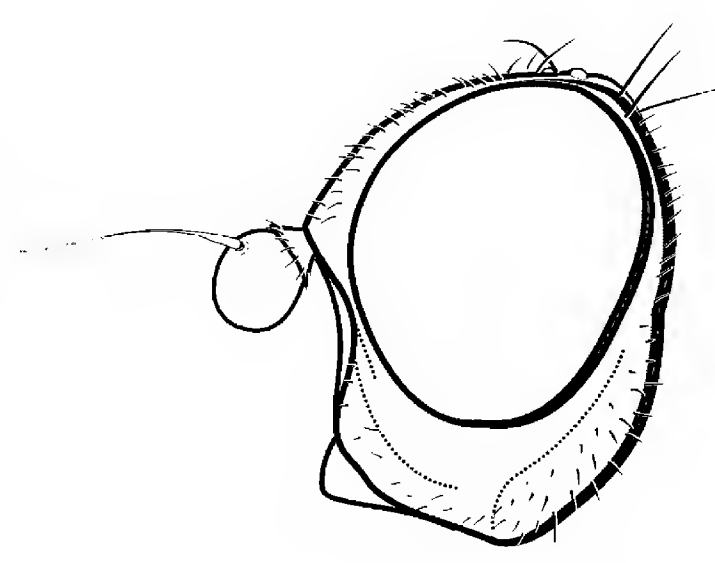
Physiphora have been reared from a decaying poplar tree, *Populus euphratica* Oliv. (Salicaceae), tips of date palm, *Phoenix dactylifera* L. (Arecaceae) consumed by the palm weevil (*Rhynchophorus* Herbst, Curculionidae) larvae and rotting *Euphorbia* (Euphorbiaceae), where fly larvae feed either on decaying plant matter or dead insect larvae (Kameneva & Korneyev 2016). Adults are attracted by compost, dung, bird droppings and carrion (Krivosheina & Krivosheina 1997*a*). Larvae of some *Timia* Wiedemann develop in rotten roots of *Cystanche* (Orobanchaceae) and *Ferula* (Apiaceae) (Mamaev 1977; Morgulis & Freidberg 2014). Flies of the tribe Lipsanini (*e.g.*, *Euxesta* Loew) are associated mostly with monocotyledons (cereals and palms), developing in tissues damaged by other insects in the New World (Steyskal 1974). Detailed synopses of existing biological data were presented by Allen & Foote (1967) and Ferrar (1987: 266), but the larval habits of the majority of species remain unknown.

In Afrotropical genera, only the immature stages of a few virtually cosmopolitan *Physiphora* species have been described and illustrated (Allen & Foote 1967). The third-instar larva (Fig. 46) is of the usual schizophoran type, with the integument smooth, lacking distinct protuberances. The prothoracic spiracle (Fig. 46) consists of 13–16 papillae on a narrow fleshy base and the abdominal segments have creeping welts ventrally (Fig. 46). The posterior spiracles (Figs 46, 48, 49) may be conspicuously elevated above the surface of terminal segment (as in Fig. 49), with the peritreme distinctly pigmented (Fig. 48). The spiracular openings (Fig. 48) are elongate, obliquely orientated, interspersed with four groups of weakly branching peristigmatic tufts and a basal ecdysial scar (Fig. 48). The cephaloskeleton (Fig. 47) is typical for other saprophagous Tephritoidea, with the mouthhooks developed into a single, long apical hook and the dental and labial sclerites are present. The intermediate sclerite (Fig. 47) is long and narrow with the basal sclerite developed into a long, needle-like parastomal bar, a narrow dorsal cornu and broader ventral cornu. The puparium (Fig. 49) is typically barrel-shaped of cyclorrhaphous form; light yellow to reddish brown, with posterior spiracles sessile or on tubular mountings (Ferrar 1987: 271).

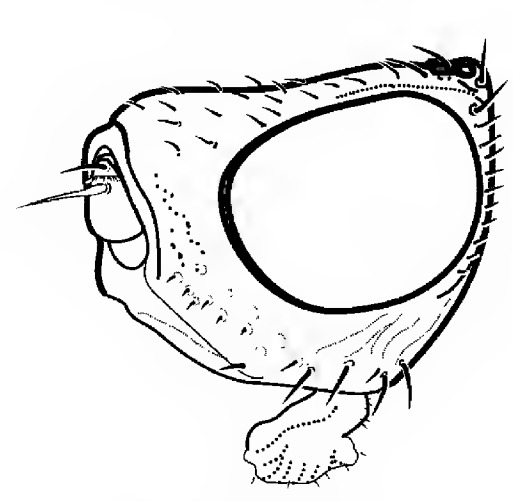
8 *Physiphora*



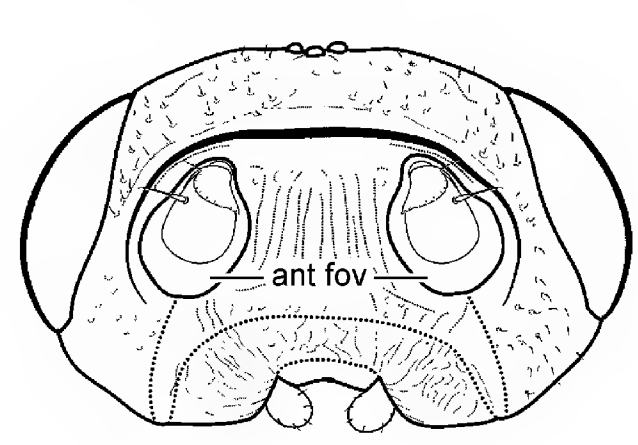
9 *Physiphora*



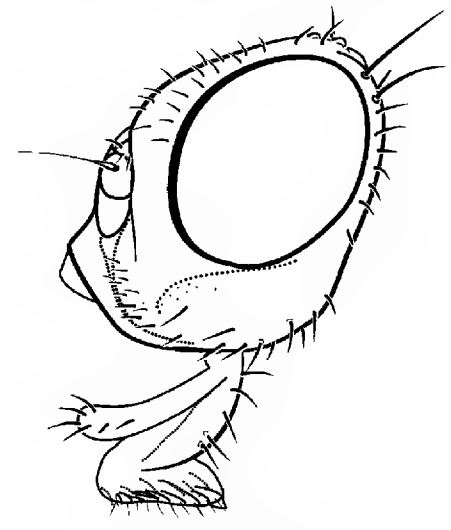
10 *Pseudeuxesta*



11 *Timia*



12 *Timia*



13 *Ulidia*

Figs 69.8–13. Heads of Ulidiidae: (8) *Physiphora clausa* (Macquart), lateral view; (9) *Ph. sericea* (Hendel), anterior view; (10) *Pseudeuxesta prima* (Osten Sacken), lateral view; (11) *Timia berlandi* Séguy, lateral view; (12) same, anterior view; (13) *Ulidia fascialis* Hendel, lateral view (non-Afrotropical). Fig. 8 (Kameneva & Korneyev 2016, fig. 94), Fig. 9 (after Kameneva & Korneyev 2010*a*, fig. 10).

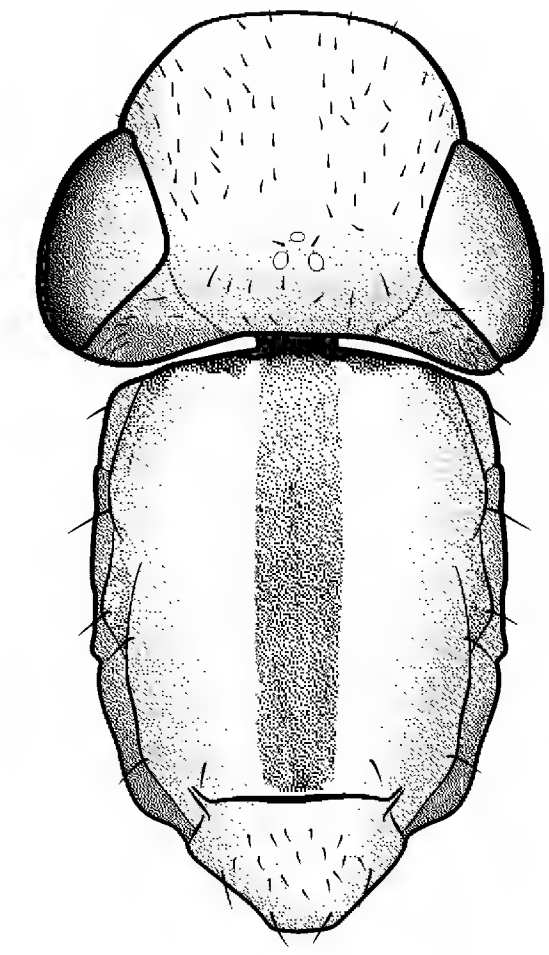
Abbreviation: ant fov – antennal foveae.

Economic significance

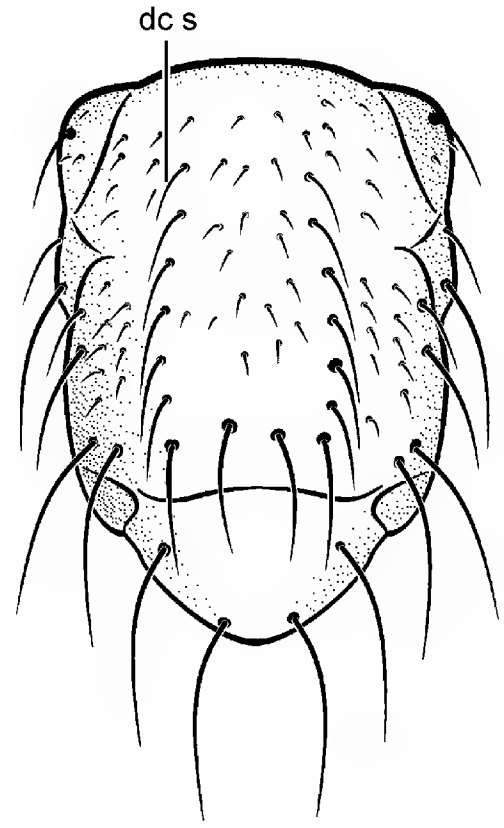
Larvae of *Pseudeuxesta prima* (Osten Sacken, 1881) were found in a human corpse, under natural conditions in the Oriental Region, on the Pacific island of Guam (Bohart & Gressitt 1951), so may have forensic significance. No other cases of economically important species of the Afrotropical picture-winged flies have been reported.

Classification

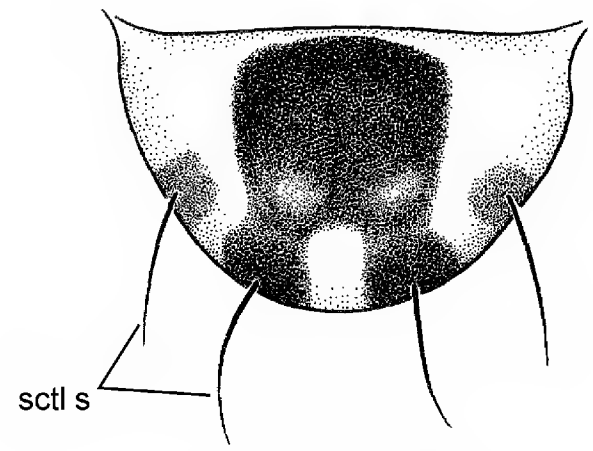
Ulidiidae are the third largest family, after Tephritidae and Platystomatidae, of the superfamily Tephritoidea. Together with these two families and Pyrgotidae, they form a monophyletic group within Tephritoidea, the so-called "higher Tephritoidea" (Korneyev 1999: 10). This group differs from the "lower Tephritoidea" by the complete lack of spiracles 6 and 7 and of



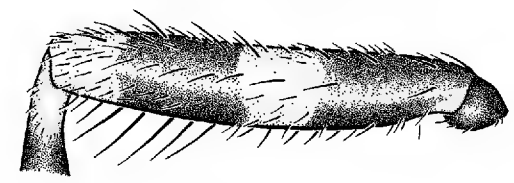
14 *Timia*



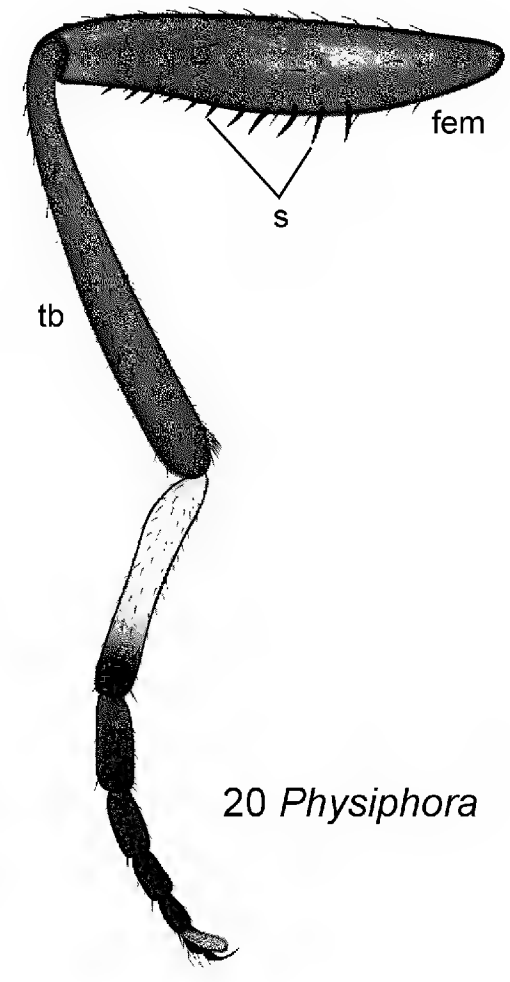
15 *Melieria*



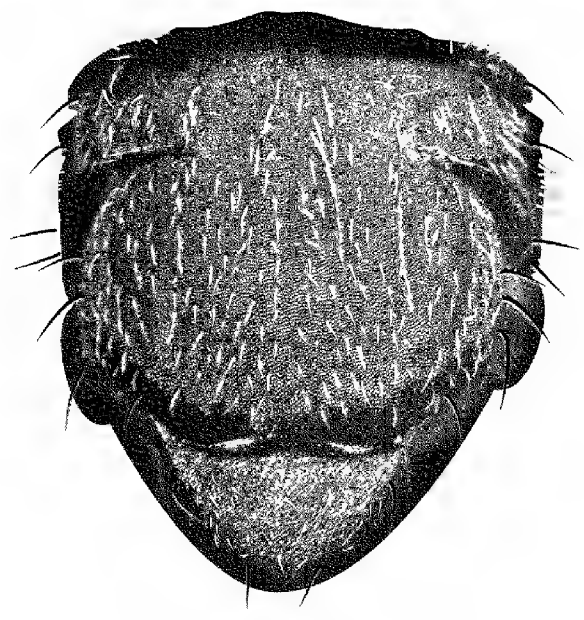
18 *Arborotites*



19 *Arborotites*



20 *Physiphora*



16 *Physiphora*

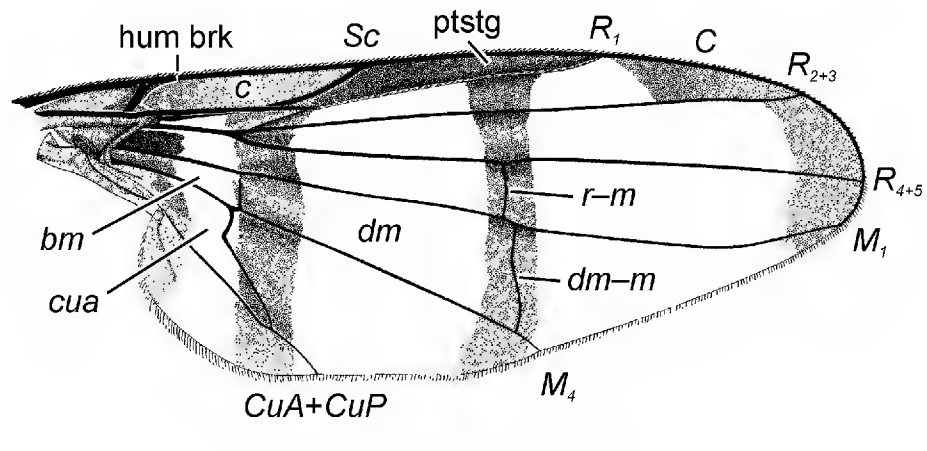
17 *Physiphora*

Figs 69.14–20. Thoracic and leg structures of Ulidiidae: (14) head and thorax of *Timia berlandi* Séguy, dorsal view; (15) mesonotum of *Melieria nigritarsis* Becker, dorsal view; (16) same, *Physiphora leucotricha* Kameneva & Korneyev, dorsal view; (17) same, *Ph. clausa* (Macquart); (18) scutellum of *Arborotites stuckenbergi* Barraclough, dorsal view; (19) same, fore femur, anterior view; (20) fore leg of *Ph. alceae* (Preyssler), anterior view. Figs 16, 17, 20 (after Kameneva & Korneyev 2010*a*, figs 15, 4, 5, respectively), Figs 18, 19 (Barraclough 2000, figs 15, 14, respectively).

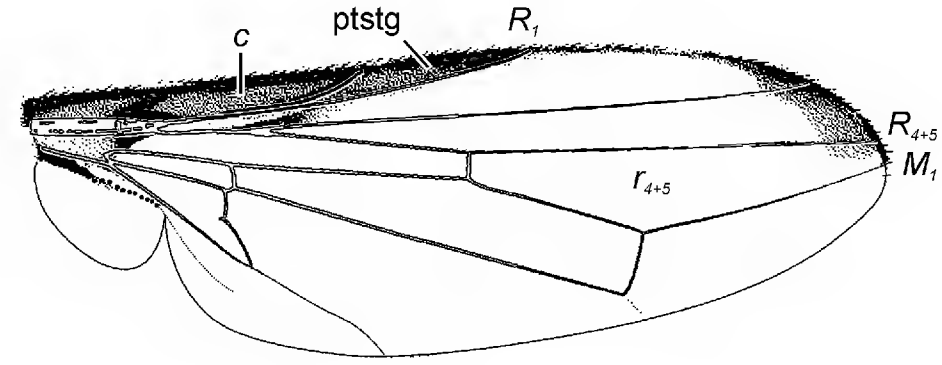
Abbreviations: dc s – dorsocentral seta; fem – femur; s – setae; tb – tibia; sctl s – scutellar setae.

setae on abdominal sternite 6 in males (McAlpine 1989: 1437, 1440). Monophyly of the family is tentative, but is supported by the absence of the presutural supra-alar seta (synapomorphy) in combination with the absence of anepimeral setulae and setae (symplesiomorphy differentiating Ulidiidae from other "higher Tephritoidea" families) (Kameneva & Korneyev 2006). In a paper by Wiegmann *et al*. (2011), the Ulidiidae also form a early branching lineage, with a monophyletic sistergroup of Platystomatidae + Tephritidae + Pyrgotidae + Ctenostylidae in the monophyletic "higher Tephritoidea", but monophyly of the Ulidiidae itself has not been shown.

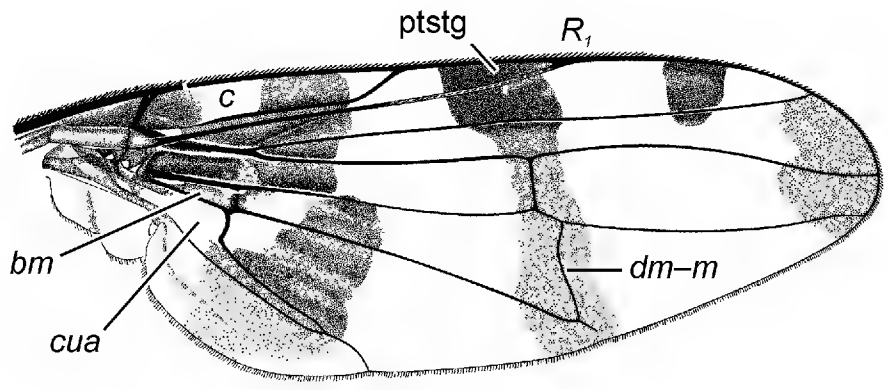
The most comprehensive and detailed review of suprageneric nomenclature and classification based upon phylogenetic



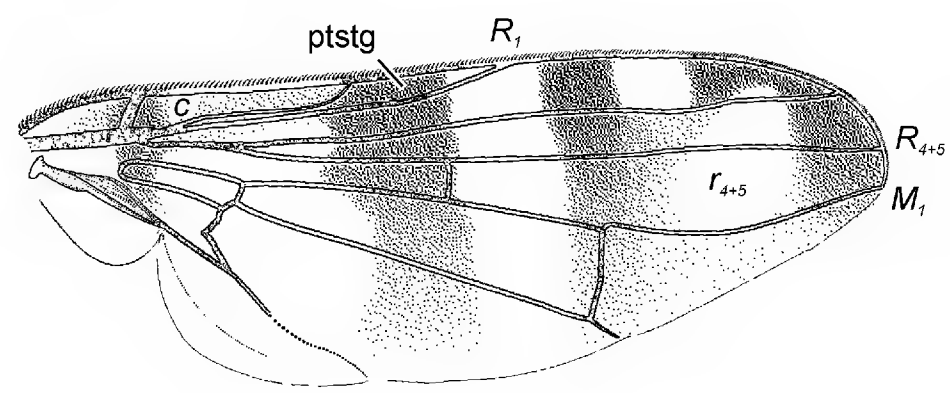
21 *Acatochaeta*



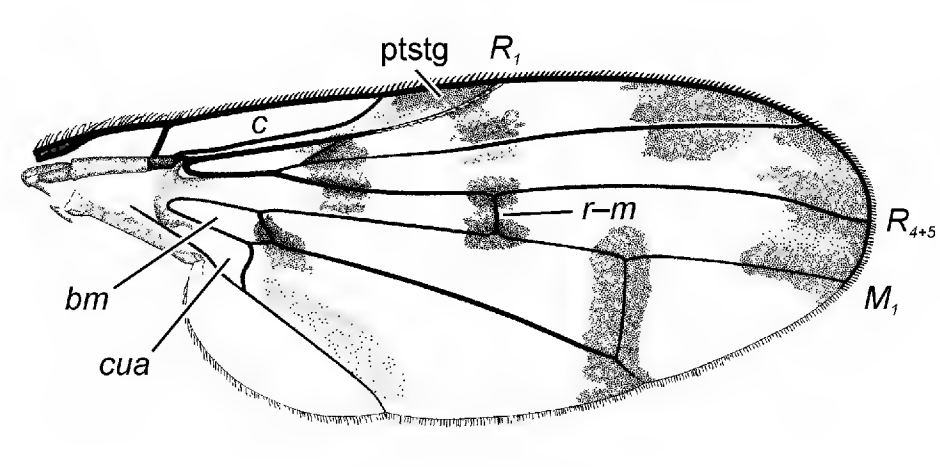
22 *Acrosticta*



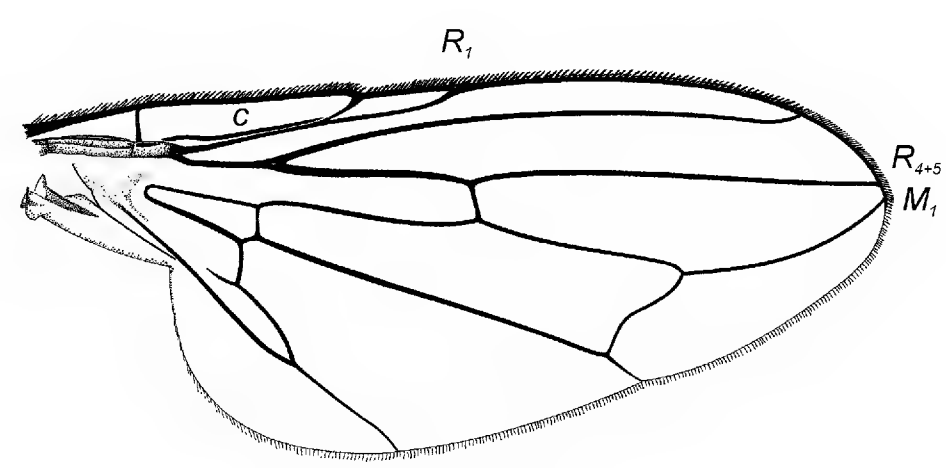
23 *Arborotites*



24 *Euxesta*



25 *Melieria*



26 *Namibotites*

Figs 69.21–26. Wings of Ulidiidae (dorsal views): (21) *Acatochaeta africana* Enderlein; (22) *Acrosticta apicalis* (Williston); (23) *Arborotites stuckenbergi* Barraclough; (24) *Euxesta eluta* Loew (non-Afrotropical); (25) *Melieria nigritarsis* Becker; (26) *Namibotites argentata* Barraclough. Figs 22, 24 (Kameneva & Korneyev 2010*b*, figs 32, 33), Figs 21, 23, 25, 26 (Barraclough 2000, figs 8–11).

Abbreviations: *bm* – basal medial cell; *c* – costal cell; *C* – costal vein; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *dm* – discal medial cell; *dm–m* – discal medial crossvein; hum brk – humeral break; M_1 – first branch of media; M_4 – fourth branch of media; ptstg – pterostigma; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; r_{4+5} – fourth + fifth radial cells; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Sc* – subcostal vein.

analysis was proposed by Kameneva & Korneyev (2006). The family was divided into two subfamilies: Ulidiinae and Otitinae. The subfamily Ulidiinae includes four tribes: the predominantly Neotropical Lipsanini (= Euxestinae, preoccupied name) and Pterocallini, the Holarctic Seiopterini and the mostly Old World Ulidiini. The subfamily Otitinae comprises three tribes: Cephaliini, Myennidini and Otitini. The majority of genera belonging to this subfamily occur in the Holarctic Realm. A few genera of Myennidini and Ulidiini are native to the Afrotropical Region (Barraclough 2000). Two genera of Lipsanini (*Acrosticta* and *Pseudeuxesta* Hendel) and *Melieria* (Otitini), are apparently invasive from the Neotropical and Palaearctic Regions, respectively.

Identification

Barraclough (2000) provided an identification key to Afrotropical genera, which includes some terminalia characters. The following identification key is largely based on that work. Ulidiidae are normally micro-pinned in the field for later double-mounted (see Chapter 2).

Key to genera of Afrotropical Ulidiidae

1. Wing vein R_1 bare or if with a few setulae in apical ¼, then vein M_1 deflected anteriorly, ending before or at wing apex (e.g., Figs 22, 24, 26–30); wing membrane usually hyaline or at most with 2 dark maculae or lacking dark pattern (e.g., Figs 26, 30). 2

– Wing vein R_1 setulose dorsally on apical part, vein M_1 parallel to vein R_{4+5}, if slightly curved anteriorly, then ending posterior to wing apex (e.g., Figs 21, 25); wing invariably with more than 2 bands or maculae (e.g., Figs 21, 23, 25) 8

2. Head, abdomen and thorax uniformly grey microtrichose; head with antennal foveae rounded, widely separated (Fig. 7) . . . . . *Namibotites* Barraclough

– Abdomen entirely shiny; head and thorax at most with microtrichose maculae or bands; head with antennal foveae either deep and separated from carina (e.g., Fig. 12), or shallow, with smooth and low carina between (e.g., Figs 3, 8–10) 3

3. Head with antennal foveae round, deep and widely separated (e.g., Fig. 12) 4

– Head with antennal foveae shallow, with smooth and low carina between (e.g., Figs 1, 3, 8–10) 5

4. Head longer and wider than high, mostly yellow (Figs 11, 12, 14); wing vein M_1 strongly deflected anteriorly, ending well before wing apex (Fig. 29) . . . . . *Timia* Wiedemann

– Head at least as high as long (Fig. 13), mostly black; wing vein M_1 reaching costal vein (*C*) almost at wing apex (Fig. 30) (non-Afrotropical). . . . . [*Ulidia* Meigen]

5. Wing membrane entirely hyaline (Fig. 27) or at most with small apical black macula; cell r_{4+5} almost or entirely closed (Fig. 27), sometimes petiolate; male terminalia with phallus bare, bearing membranous caeca and a glans-like structure, composed of sclerotised sub-apical hooks (Fig. 35); female syntergite 1 + 2 with pair of bare and matt dimple-like structures (Fig. 44); 3 spermathecae present (Fig. 43) . . . . . *Physiphora* Fallén

– Wing membrane with dark maculae (e.g., Figs 22, 24) or banded (e.g., Fig. 28); cell r_{4+5} moderately narrowed, but not closed at apex (e.g., Figs 22, 24, 28); male terminalia with phallus simple, without glans-like structure, bare or uniformly short microspinulose (e.g., Fig. 38); female syntergite 1 + 2 without dimple-like structures; 2 spermathecae present (e.g., Fig. 39). 6

6. Head with frons rugose (Fig. 4); wing with pterostigma longer than ½ length of costal cell (*c*) (Fig. 22) . . . . . *Acrosticta* Loew

– Head with frons smooth; wing with pterostigma shorter than ½ length of costal cell (*c*) (e.g., Figs 24, 28). 7

7. Wing with dorsal surface of vein R_1 setulose distal to apex of subcostal vein (*Sc*) (Fig. 28) . . . . . *Pseudeuxesta* Hendel

– Wing with dorsal surface of vein R_1 entirely bare (Fig. 24) (non-Afrotropical). . . . . [*Euxesta* Loew]

8. Wing with pterostigma ½ as long as costal cell (*c*); vein R_1 ending at level of crossvein *r–m*; section of vein M_1 between crossveins *r–m* and *dm–m* much longer than *r–m*; posteroapical lobe of cell *cua* less than ½ as long as cell *bm* (Fig. 25); thorax with mesonotum with row of 1 presutural and 2–6 postsutural dorsocentral setae (Fig. 15) . . . . . *Melieria* Robineau-Desvoidy

– Wing with pterostigma as long as or longer than costal cell (*c*); vein R_1 ending at level of crossvein *dm–m*; section of vein M_1 between crossveins *r–m* and *dm–m* shorter than *r–m*; posteroapical lobe of cell *cua* as long as or longer than cell *bm* (e.g., Figs 21, 23); thorax with mesonotum with 1 postsutural dorsocentral seta 9

9. Scutellum flattened, with 1 pair of scutellar setae; body uniformly brownish; femora not banded. . . . . .*Acatochaeta* Enderlein

– Scutellum rounded, convex, with 2 pairs of scutellar setae (Fig. 18); body speckled with brown and grey pattern; femora black with yellow bands (Fig. 19) . . . . . .*Arborotites* Barraclough

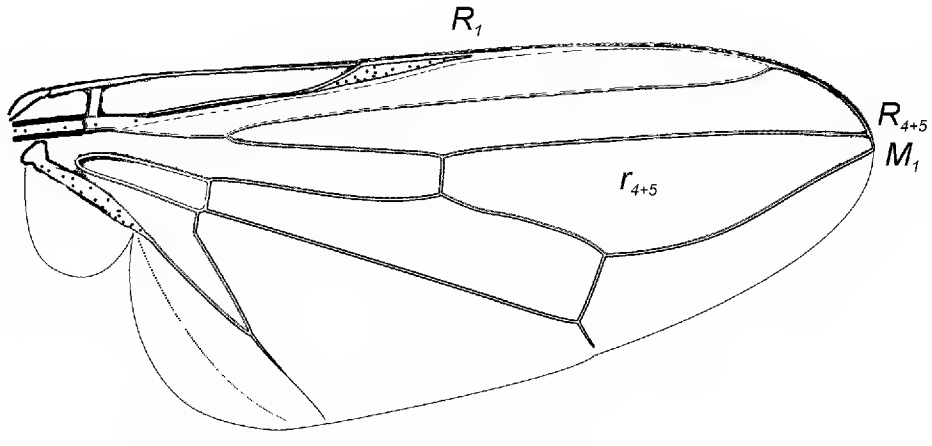
Synopsis of the fauna

***Acatochaeta* Enderlein** (Otitinae: ?Myennidini)**.** An endemic monotypic genus. The single species, *A. africana* Enderlein, 1921, is large (body length: 10–12 mm), with a banded wing pattern (Fig. 21) and is recorded from Equatorial Guinea and Kenya (Barraclough 2000). Larvae are unknown, but may possibly develop in rotten wood.

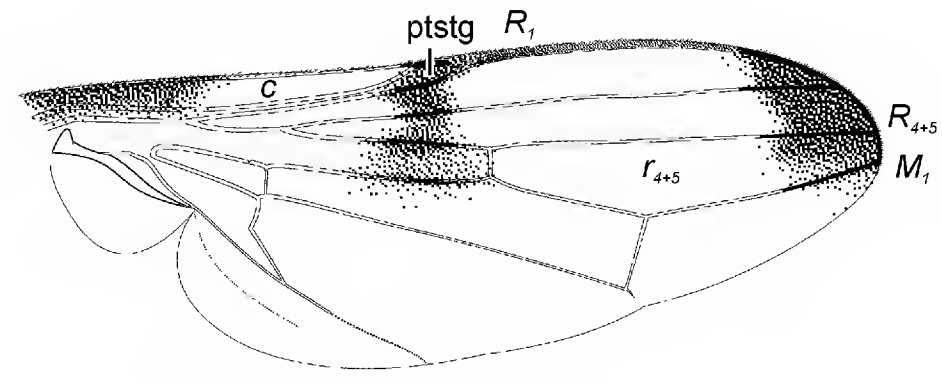
***Acrosticta* Loew** (Ulidiinae: Lipsanini)**.** A genus of 14 described species, occurring in the Nearctic and Neotropical Regions; only the virtually cosmopolitan species, *A. apicalis* (Williston, 1896), occurs in the Afrotropical Region and is known to be introduced into Côte d'Ivoire, Liberia, Madagascar, Mauritius, Seychelles, South Africa and Tanzania; as well as Australia and Oceania (Barraclough 2000; Steyskal 1968: 54.13). The species has the frons deeply pitted or wrinkled (Fig. 4); the wing usually with dark fascia along the anterior margin, from the base to the apex of vein R_1 (Fig. 22). The epandrium of the male terminalia is rounded and the surstyli lack prensisetae (Fig. 38). Tergites 4–6 of the female abdomen are narrowed and the spiracles are displaced onto the dorsal side, 2 spermathecae are present (Fig. 39) and the aculeus is moderately narrow, oval in profile (not flattened dorsoventrally), with an oval cercal unit (Fig. 41). Larvae remain unknown.

***Arborotites* Barraclough** (Otitinae: Myennidini)**.** An endemic monotypic genus, with the single species, *A. stuckenbergi* Barraclough, 2000. This species is moderately large (body length: 6–8 mm) and is recorded from South Africa and Zimbabwe. Adults have been collected (often *in copula*) on shaded tree trunks and adjacent litter in wooded and forested areas (Barraclough 2000) and roosting beneath rock overhangs in South Africa (A.H. Kirk-Spriggs, pers. comm. 2014). Larvae remain unknown, but possibly develop in rotten wood.

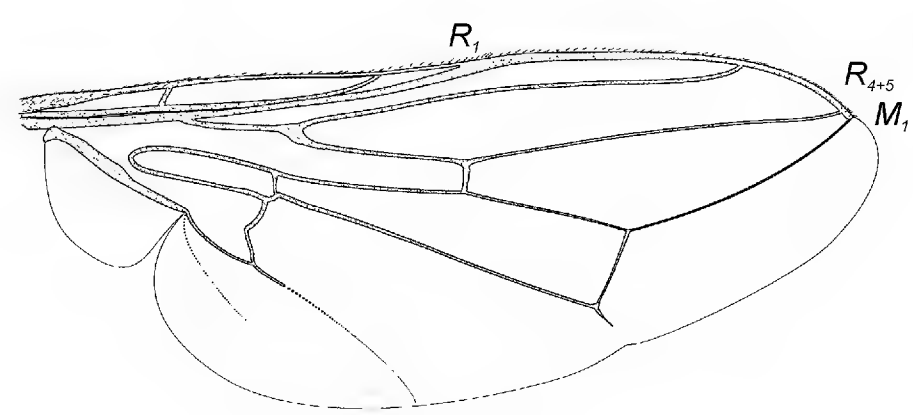
[***Euxesta* Loew** (Ulidiinae: Lipsanini)**.** A genus of 90 described species native to the New World and Pacific islands (Kameneva 2004), with a few species accidentally introduced into Europe and Asia. The genus is not recorded from the Afrotropical Region, but may possibly occur there. Larvae of several species infest ears of corn, some develop in the rotting bast fibres of



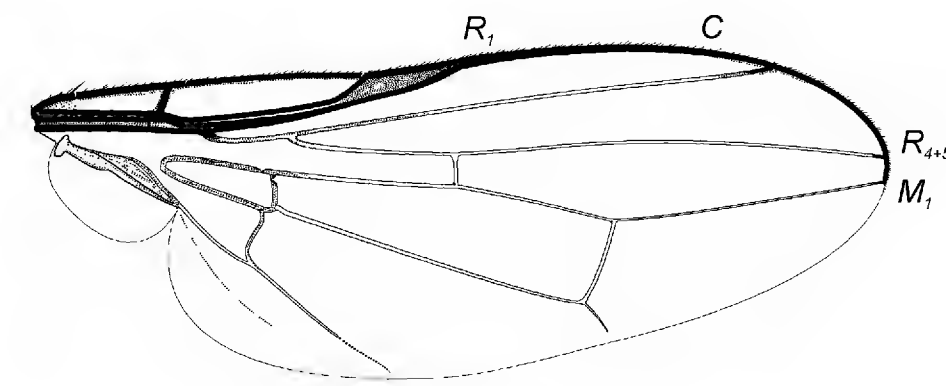
27 *Physiphora*



28 *Pseudeuxesta*



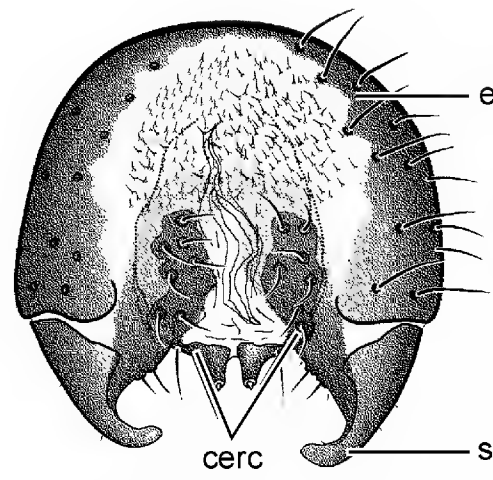
29 *Timia*



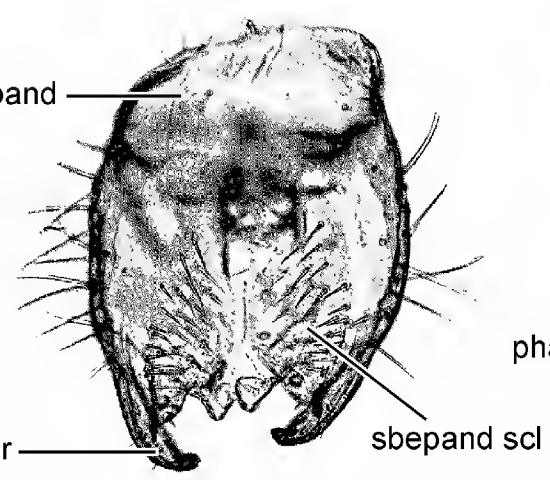
30 *Ulidia*

Figs 69.27–30. Wings of Ulidiidae (dorsal views): (27) *Physiphora sericea* (Hendel); (28) *Pseudeuxesta prima* (Osten Sacken); (29) *Timia berlandi* Séguy; (30) *Ulidia fascialis* Hendel (non-Afrotropical).

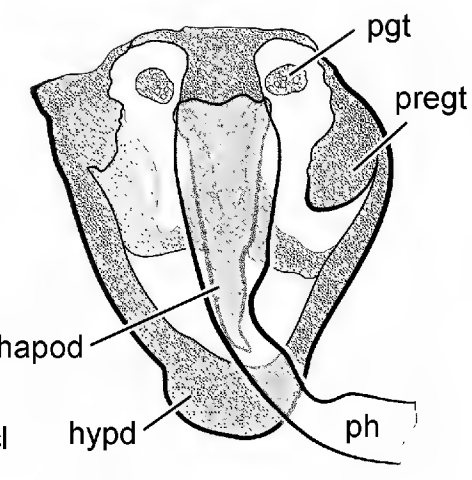
Abbreviations: *c* – costal cell; *C* – costal vein; M_1 – first branch of media; ptstg – pterostigma; R_1 – anterior branch of radius; r_{4+5} – fourth + fifth radial cells; R_{4+5} – third branch of radius.



31 *Physiphora* ♂

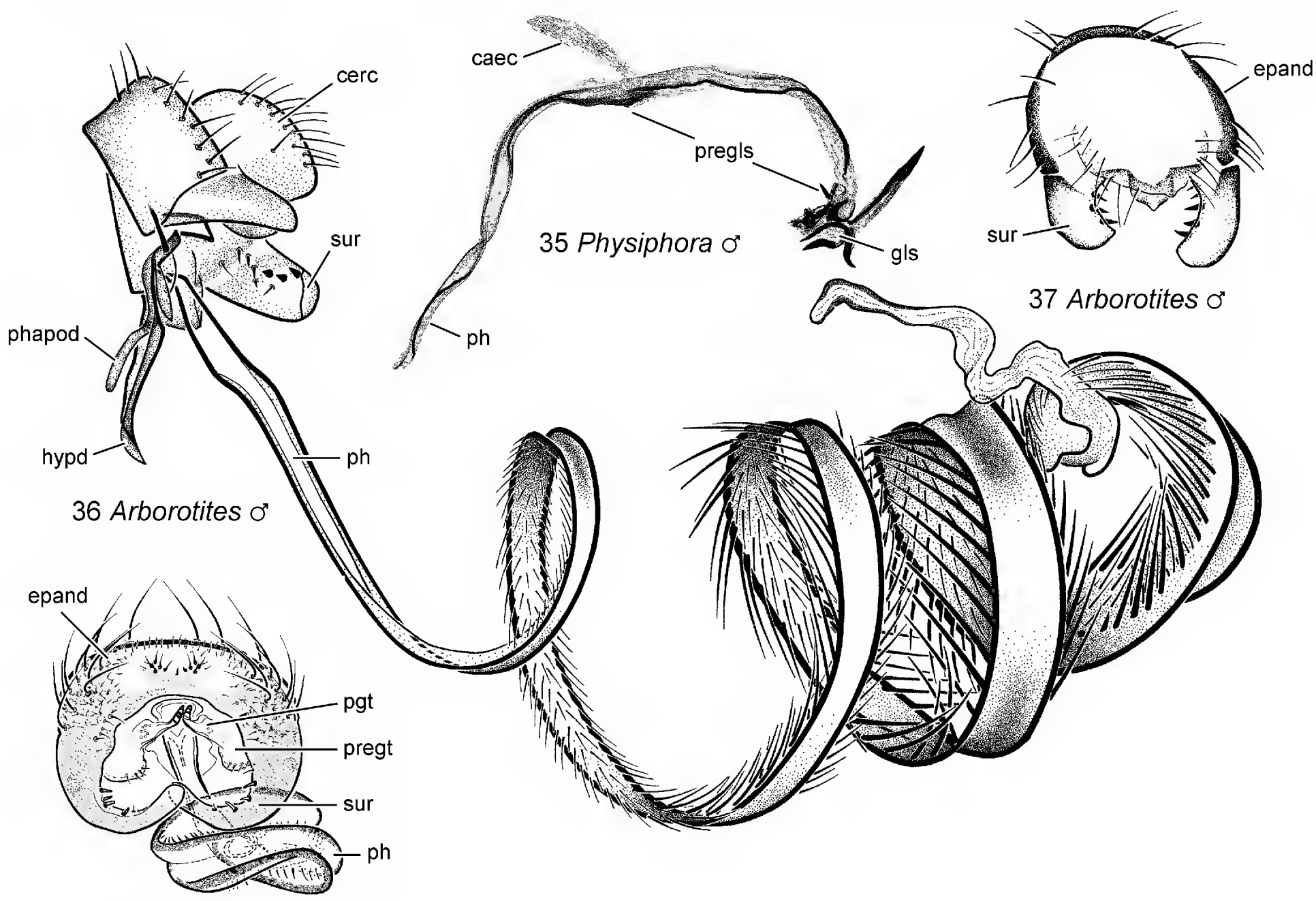


32 *Physiphora* ♂



33 *Physiphora* ♂

34 *Physiphora* ♂



35 *Physiphora* ♂

36 *Arborotites* ♂

37 *Arborotites* ♂

38 *Acrosticta* ♂

Figs 69.31–38. Male terminalia of Ulidiidae: (31) epandrium and surstylus of *Physiphora alceae* (Preyssler), caudal view; (32) same, *Ph. clausa* (Macquart), anterior view; (33) same, hypandrium, ventral view; (34) same, phallus glans, lateral view; (35) phallus of *Ph. smaragdina* (Loew), lateral view; (36) male terminalia of *Arborotites stuckenbergi* Barraclough, lateral view; (37) same, epandrium, posterior view; (38) male terminalia of *Acrosticta profunda* Hendel, ventral view. Fig. 31 (Chen & Kameneva 2007, fig. 6), Figs 32–34 (after Kameneva & Korneyev 2010*a*, figs 32, 34, 35), Fig. 35 (Kameneva & Korneyev 2016, fig. 346), Figs 36, 37 (Barraclough 2000, figs 19, 18, respectively), Fig. 38 (Kameneva & Korneyev 2010*b*, fig. 24).

Abbreviations: caec – caecum; cerc – cercus; epand – epandrium; gls – glans; hypd – hypandrium; pgt – postgonite; ph – phallus; phapod – phallapodeme; pregls – preglans; pregt – pregonite; sbepand scl – subepandrial sclerite; sur – surstylus.

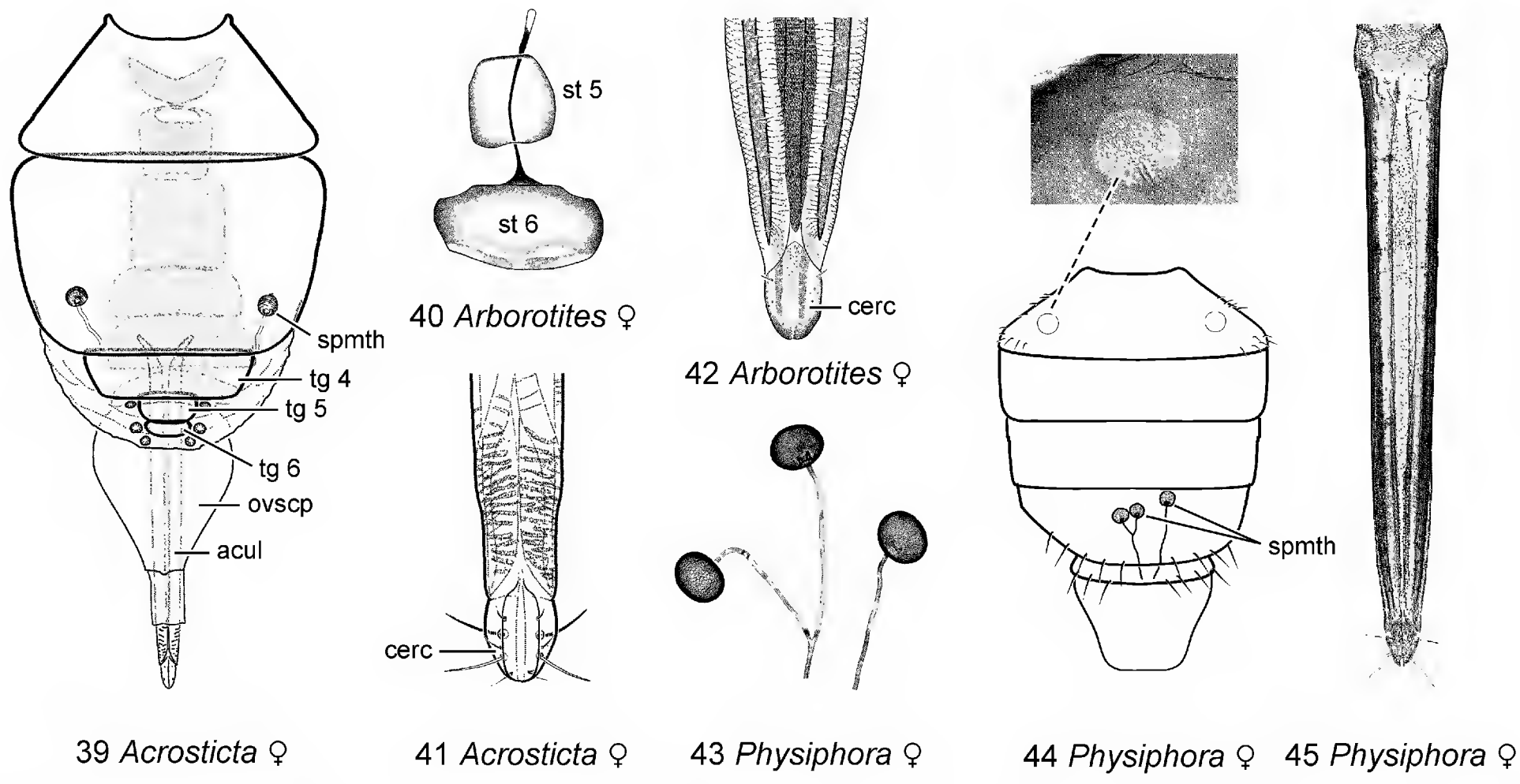
trees and in developing shoots of palms (see Kameneva & Korneyev 2010*b*, for references). The most recent identification key to species (*i.e.*, Curran 1935) is in need of revision.]

Melieria **Robineau-Desvoidy** (Otitinae: Otitini)**.** A mainly Palaearctic genus of *ca* 40 described species. One species, *M. nigritarsis* Becker, 1903, occurring in Eurasian xeric areas, has also has been recorded from Angola, Kenya, Namibia and Nigeria (Barraclough 2000) and from Saudi Arabia and United Arab Emirates in the Arabian Peninsula (Kameneva & Korneyev 2010*a*: 633). Species of the genus are often collected in association with plants of the genera *Artemisia* (Asteraceae), *Phragmites* (Poaceae) and *Typha* (Typhaceae), on riverbanks and along sea shores; the larvae possibly developing in decaying plant material (Kabos & Aartsen 1984). The immature stages remain unknown.

Namibotites **Barraclough** (Otitinae: Myennidini)**.** An endemic monotypic genus, with the single species, *N. argentata* Barraclough, 2000, described from Namibia. This is a medium-sized species (body length: 4–6 mm), with a densely grey microtrichose body and hyaline wings (Barraclough 2000). The immature stages and biology remain unknown.

Physiphora **Fallén** (Ulidiinae: Ulidiini)**.** Twenty-seven (of *ca* 30 species) occur in the Afrotropical Region (Kameneva & Korneyev 2010*a*: 616, 2016), with the two virtually cosmopolitan, synanthropic species, *Ph. alceae* (Preyssler, 1791) and *Ph. clausa* (Macquart, 1843), having been introduced into the New World and Australia, and three species found only in the Oriental and Australasian Regions. Mostly black or brown flies, with hyaline wings; thorax and abdomen usually with a metallic green, blue or purple sheen, often glossy or shagreened (Figs 1, 16, 17); abdomen rarely dull black. Adults are often attracted to faeces, avian droppings, reptilian and mammalian dung, carrion, rotting fruits and compost. Krivosheina & Krivosheina (1997*a*) reported about larvae found beneath bark of a dead desert poplar, *Populus euphratica* Oliv. (Salicaceae), in Turkmenistan and in rotting tissues of the succulent shrub *Euphorbia royleana* Boiss. in India and Pakistan and assumed *Physiphora* larvae to be necrozoophagous. Larvae of *Ph. alceae*, *Ph. allomma* (Speiser, 1914), *Ph. clausa*, *Ph. longicornis* (Hendel, 1909) and *Ph. violacea* (Hendel, 1910) infest growing tips or feed in the rotting stems of palms, mainly of the date palm, possibly in association with the burrow froth and frass of the palm weevils *Rhynchophorus ferrugineus* (Olivier 1790), which is believed to be common for most widespread *Physiphora* species (Kameneva & Korneyev 2016). Larvae are described for *Ph. alceae* (Allen & Foote 1967) and *Ph. chalybea* (Hendel, 1909) (Krivosheina & Krivosheina 1997*a*). Kameneva & Korneyev (2016) recently revised the genus and provided an identification key to all Afrotropical species.

Pseudeuxesta **Hendel** (Ulidiinae: Lipsanini)**.** One species, *Ps. prima*, of Pacific origin, also occurring in South-east Asia



39 *Acrosticta* ♀ 40 *Arborotites* ♀ 41 *Acrosticta* ♀ 42 *Arborotites* ♀ 43 *Physiphora* ♀ 44 *Physiphora* ♀ 45 *Physiphora* ♀

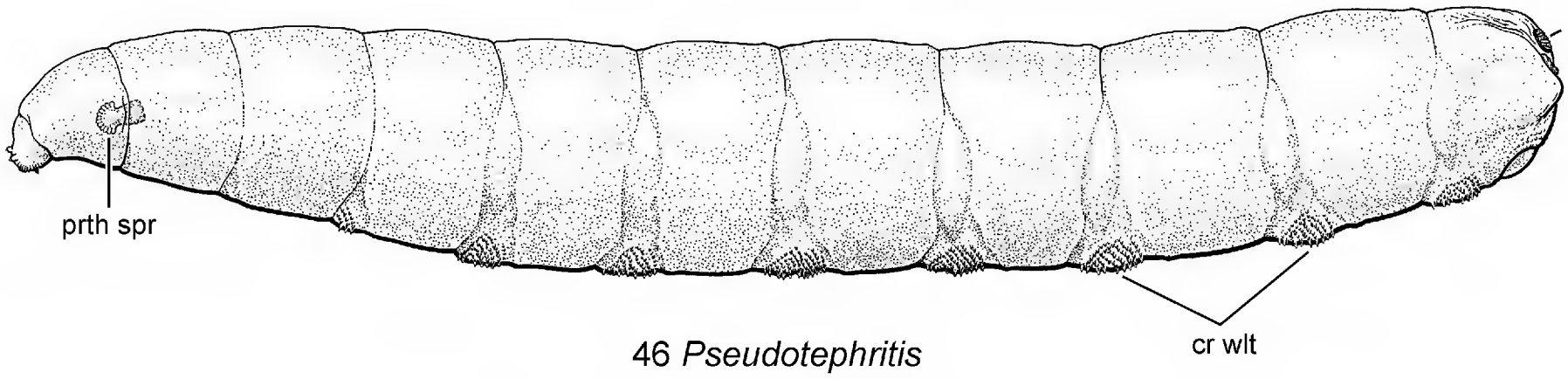
Figs 69.39–45. Female abdomen and terminalia of Ulidiidae: (39) abdomen of *Acrosticta profunda* Hendel, dorsal view; (40) sternites 5 and 6, with anteromedial apodeme of *Arborotites stuckenbergi* Barraclough, ventral view; (41) enlarged apex of aculeus of *Ac. profunda*, ventral view; (42) aculeus of *Ar. stuckenbergi*, ventral view; (43) spermathecae of *Physiphora alceae* (Preyssler), dorsal view; (44) female abdomen of *Ph. sericea* (Hendel), dorsal view (inset enlarged fragment of tergite 2); (45) same, aculeus, ventral view. Figs 39, 41 (Kameneva & Korneyev 2010*b*, figs 20, 21), Figs 40, 42 (Barraclough 2000, figs 22, 20, respectively), Figs 43–45 (Kameneva & Korneyev 2016, figs 40, 333, 334).

Abbreviations: acul – aculeus; cerc – cercus; ovscp – oviscape; spmth – spermatheca; st – sternite; tg – tergite.

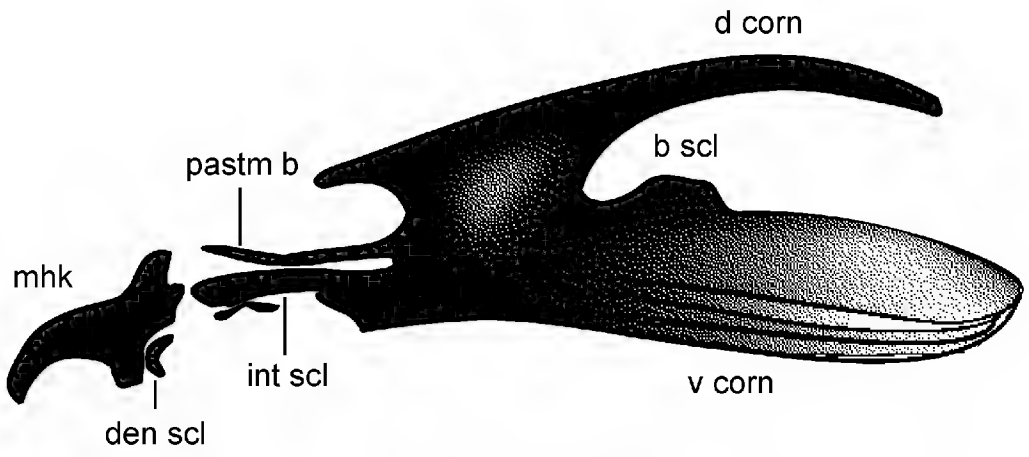
and Australia, is recorded from Kenya, Madagascar and Seychelles in the Afrotropical Region (Barraclough 2000). The species is reported as being necrophagous (Bohart & Gressitt 1951), but possibly uses a wider range of decomposing organic matter for larval development. The immature stages of the species remain unknown.

***Timia* Wiedemann** (Ulidiinae: Ulidiini)**.** An almost exclusively Palaearctic genus, with more than 60 described or recognised species (Galinskaya 2011*b*, 2014; Morgulis & Freidberg 2014; Zaitzev 1984: 422). One species, *T. berlandi* Séguy, 1953, occurs in xeric areas of Mauritania and Egypt (Sinai) and has been reared from the rotten shoots of *Cystanche* (Orobanchaceae) (Morgulis & Freidberg 2014). Adults are often attracted to faeces, avian droppings and decomposing plant matter. The immature stages remain unknown. The most recent identification key was presented by Morgulis & Freidberg (2014) and partly by Galinskaya (2011*b*, 2014).

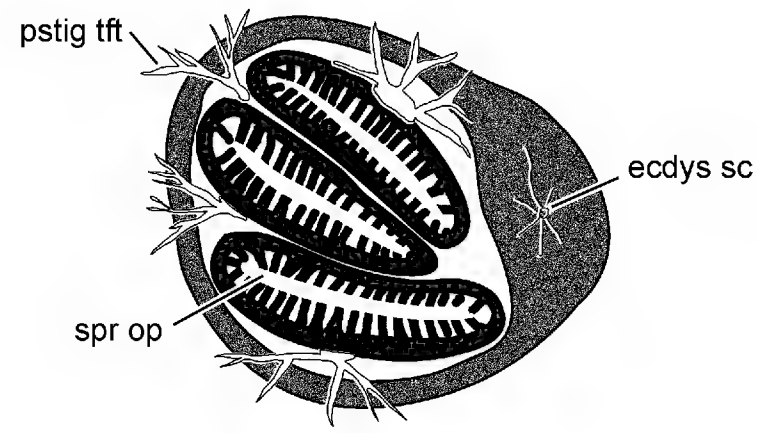
[***Ulidia* Meigen** (Ulidiinae: Ulidiini)**.** A Palaearctic genus of 24 described or recognised species (Chen & Kameneva 2009; Galinskaya 2011*a*; Kameneva 2008; Morgulis & Freidberg 2014).



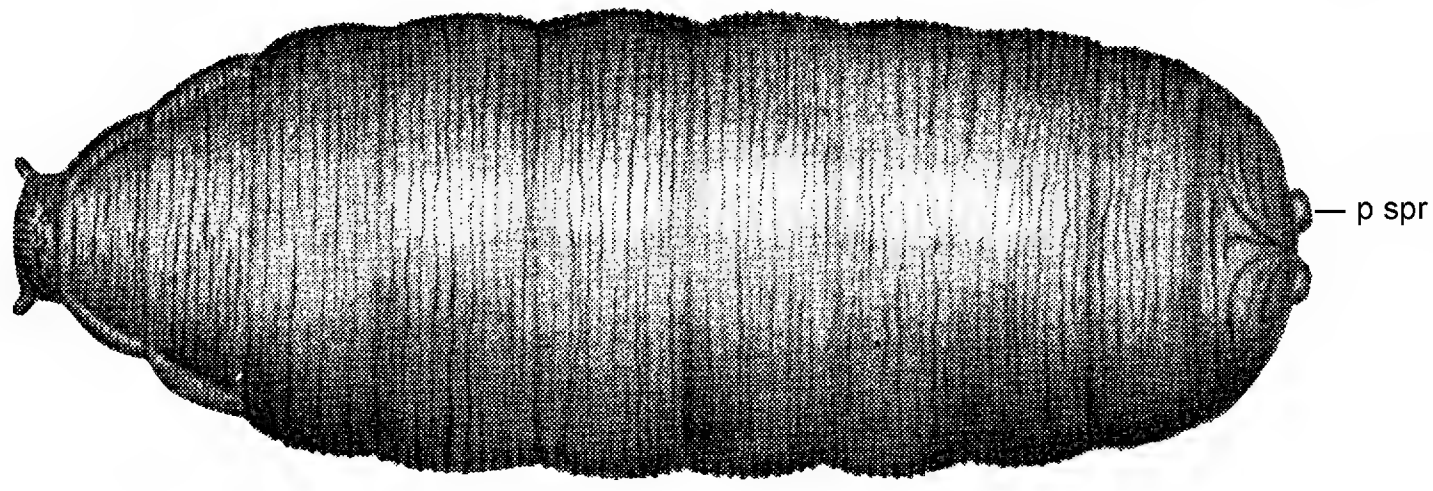
46 *Pseudotephritis*



47 *Physiphora*



48 *Physiphora*



49 *Physiphora*

Figs 69.46–49. Immature stages of Ulidiidae: (46) habitus of third-instar larva of *Pseudotephritis corticalis* (Loew), lateral view (non-Afrotropical); (47) cephaloskeleton of third-instar larva of *Physiphora alceae* (Preyssler), lateral view; (48) same, posterior spiracle, caudal view; (49) puparium of *Ph. clausa* (Macquart), dorsal view. Fig. 46 (Steyskal 1987, fig. 30), Figs 47, 48 (after Hennig 1940, figs 9, 10), Fig. 49 (Bohart & Gressitt 1951, Plate 10, as *Chrysomyza aenea*).

Abbreviations: b scl – basal sclerite; cr wlt – creeping welts; d corn – dorsal cornu; den scl – dental sclerite; ecdys sc – ecdysial scar; int scl – intermediate sclerite; mhk – mouthhook; p spr – posterior spiracle; pastm b – parastomal bar; prth spr – prothoracic spiracle; pstig tft – peristigmatic tuft; spr op – spiracular opening; v corn – ventral cornu.

Ulidia apicalis Meigen, 1826, *U. facialis* Hendel, 1931, *U. megacephala* Loew, 1845 and *U. wadicola* Steyskal, 1968, occur in Egypt, Morocco and Tunisia in North Africa and may possibly occur in the northern parts of the Afrotropical Region. Adults are often attracted to faeces, avian droppings, reptilian and mammalian dung, carrion and decomposing plant matter. The immature stages remain unknown. The most recent identification key was presented by Morgulis & Freidberg (2014).]

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PLATYSTOMATIDAE 70

(Signal Flies)

Andrew E. Whittington and Ashley H. Kirk-Spriggs

Fig. 70.1. Male of *Engistoneura stictica* (F.) (Tanzania) (photograph © S.A. Marshall).

Diagnosis

Small- to large-sized (body length: 1.7–23.0 mm; wing span: 5.0–50.0 mm) acalyptrate flies; body form ranging from small, slender (Fig. 3), to large, robust species (Figs 1, 2, 8–10); body colouration various (black, grey, brown and/or yellow), often with metallic lustre (Figs 4–6) and wing usually patterned with dark maculae or fasciae.

Head shape often modified (McAlpine 1973*b*, 1975, 1979: 221, 1982: 665, 1994; Whittington 2003, 2006), with either frons and face bulging forwards (Figs 2, 14, 16, 47, 55), or gena swollen, extending outwards (Figs 18, 46, 61, 63, 64, 72) or backwards (Figs 14, 20, 34, 39, 40, 41, 44, 51), sometimes with eye-stalks (Fig. 59); head higher than long; ocelli present (except in *Bromophila* Loew; Figs 2, 60); frontal and proclinate orbital setae absent; 0 (Figs 73–75), 1 or 2 reclinate orbital setae present (Figs 77, 78); inner and outer vertical setae present in most genera (Figs 65, 66); genal seta present; vibrissa absent or undifferentiated; postocellar setae weak, divergent; lateral postocular setae present (Fig. 74) in some genera (*Elassogaster* Bigot, *Plagiostenopterina* Hendel, *Pseudepicausta* Frey and *Rivellia* Robineau-Desvoidy); antennal pedicel with dorsal seam; postpedicel stout to elongate, sometimes with apical point; arista finely setose, pubescent (Fig. 83) and uniseriate or bipectinate (Fig. 84), apically spatulate in males of some genera (*e.g.*, *Elassogaster*, *Plagiostenopterina* (Fig. 75) and *Pseudoscholastes* Frey (Fig. 76)); proboscis stout, with broad lamella; palpus well-developed.

Thorax usually longer than broad; setae present (1 pair each, unless stated): postpronotal seta, notopleural setae (2 pairs); anepisternal seta (Fig. 85); postsutural supra-alar seta; postalar seta; intra-alar seta; prescutellar acrostichal seta; prescutellar dorsocentral seta; basal (sometimes), lateral and apical scutellar setae; katepisternal seta present in the subfamilies Scholastinae (Fig. 85) and Trapherinae. Wing (*e.g.*, Fig. 92) with membrane usually with pigmented pattern; humeral break in costal vein (*C*) present, subcostal break absent; veins R_1 and often R_{4+5} dorsally setulose for almost entire length; cell *cua* sub-rectangular at apex; before reaching crossvein *r–m*; vein M_1 either straight (Figs 98, 99, 120, 130) or convexly curved into cell *dm* (Figs 97, 121, 129, 131). Legs moderately developed, sometimes with armature (Figs 145, 146), spines (Figs

147, 148, 153) or setae (Figs 149, 155) set on tubercles; tibiae without pre-apical dorsal setae; apical ventral mid tibial spur sometimes well-developed.

Abdomen sub-cylindrical to narrow ovate; 5 pairs abdominal spiracles in male, 7 pairs in female (McAlpine 1998*b*: 193); sternites 1 and 2 separate; male postabdomen (Fig. 156) with sternite 6 reduced or absent; sternites 7 and 8 fused; lateral surstylus fused to epandrium, sheathing medial surstylus, which may also be partly fused, bearing apical peg-like prensisetae; ejaculatory apodeme with heavily sclerotised bilobed cap; phallapodeme present, sometimes reduced; phallus long, slender, uncoiled, usually terminating in sclerotised capsular glans with 2 filaments attached (in most genera), ending

Figs 70.2–7. Photographs of living Afrotropical Platystomatidae: (2) *Bromophila caffra* (Macquart) ♂ (Namibia); (3) *Conopariella tibialis* (Hendel) ♂ (Tanzania); (4) *Elassogaster* sp. ♂ (South Africa); (5) *Elassogaster* sp. ♂ (Madagascar); (6) *Naupoda* sp. ♂ (Madagascar); (7) *Oeciotypa hendeli* Lindner ♂ (Tanzania). Figs 2–7 (photographs © S.A. Marshall).

in gonopore; female postabdomen (Fig. 157) with segment 6 reduced or absent (if vestigial concealed beneath tergite 5); segment 7 present as conical oviscape, generally laterally carinate, forming rigid base to eversible ovipositor membrane that enables retraction of aculeus (by invagination) into abdominal cavity; aculeus having sensory setae apically on either side; 3 sub-spherical to ovoid spermathecae present, in conformation 2 + 1, often with complex terminal vesicles (Fig. 158).

Adult Platystomatidae are frequently confused with other "higher Tephritoidea". The absence of fronto-orbital setae, the lack of any extension of the posterior apical angle of the anterior cubital cell (*cua*) and the presence of setae along the entire length of wing vein R_1, frequently vein R_{4+5} and sometimes *Cu*, distinguishes Platystomatidae from most Tephritidae (see Chapter 71), Pyrgotidae (see Chapter 72) and Ulidiidae (see Chapter 69). By contrast, Tephritidae have between one and ten frontal setae and a subcostal break at the wing margin. Some

Figs 70.8–13. Photographs of living Afrotropical Platystomatidae: (8) *Peltacanthina* (*P.*) *mythodes* Hendel ♀ (South Africa); (9) *P.* (*P.*) *splendida* Hendel ♂ (Tanzania); (10) *P.* (*P.*) *fumipennis* Hendel ♂ (Tanzania); (11) *Plagiostenopterina* sp. courtship-pair (Namibia); (12) *Rivellia* sp. ♀ (Namibia); (13) *Scholastes cinctus* (Guérin-Méneville) ♂ (non-Afrotropical). Figs 8–12 (photographs © S.A. Marshall), Fig. 13 (photograph © D. Martiré).

confusion is possible between Plastotephritinae and Tephritidae because in both the subcostal vein (*Sc*) is abruptly bent up to the costal vein (*C*) and both have vein R_1 dorsally setulose. Representatives of Plastotephritinae can be distinguished by having vein R_{4+5} dorsally setulose, whereas vein R_{4+5} is bare dorsally in Tephritidae. Furthermore, Ulidiidae have the postocellar setae more strongly developed and the phallus coiled. Pyrgotidae often have a proepisternal ridge bearing strong setae (absent in all Platystomatidae) and lack ocelli.

Biology and immature stages

Many Platystomatidae occur in forest and forest margin habitat types (details provided for Plastotephritinae by Whittington 2003, table 5), preferring shaded, densely vegetated locations, while a few are known from grassland or agricultural environments (Whittington 2000*b*), sand dunes and other vegetation types (McAlpine 2001); further details are provided in the "Synopsis of the fauna" sections below. Some genera are to be found resting on the underside of foliage (McAlpine 1998*b*: 196; A.E. Whittington, pers. obs.), while others utilise cryptic colouration and speckled wing patterns to escape detection on bark or rock surfaces (McAlpine 1998*b*: 196).

Adults may be attracted to malodorous substances and decay, including faeces, dung, sap runs, decaying fruit and even human sweat in the case of *Lamprogaster* Macquart (non-Afrotropical) and *Rivellia* (McAlpine 1998*b*: 196). McAlpine (2001) mentioned parasitism by Stylopidae in the genus *Paryphodes* Speiser, from Papua New Guinea and by ascoma of the ectoparasitic fungus Laboulbeniales on the abdomen of a *Rivellia* species from Jervis Bay, Australia. Protein bait traps for collecting Tephritidae also attract Platystomatidae, most likely due to fermenting processes taking place which result in the same malodorous attractiveness (M. de Meyer, pers. comm. 2020).

The biology of Platystomatidae is generally poorly known and biological details for few species have been reported. Some genera have attracted detailed study, due to their elaborate sexual displays, involving waving of the wings held up at acute angles in signalling gestures for sexual courtship, hence the vernacular name "signal flies" as first applied by McAlpine (1998*a*: 111, 2000, 2001). Similar wing movements have been observed during walking or when the insect is alert (McAlpine 1973*a*, 2000). Modifications of the head and fore legs lead to further development of sexual dimorphism and agonistic behaviour for courtship (McAlpine 1973*b*, 1975, 1979: 221; Michelmore 1928; Papasogli 1973; Whittington 2006). At rest the wings are sometimes held tent-like over the abdomen, folded longitudinally or held flat (McAlpine 1998*b*: 196) and in some genera with a strong flexion line across the wing, the wing is bent over the abdomen (*e.g.*, numerous Plastotephritinae (Whittington 2003); *Lule* Speiser (Trapherinae), *Lulodes* Enderlein (Platystomatinae) and *Naupoda* Osten Sacken (Scholastinae)).

In addition to wing-waving, transfer of fluids from the mouthparts of males to those of females (trophallaxis) was observed by Foote (1985) in the Nearctic species *Rivellia pallida* Loew, 1873. Foote (1985) reported that copulation in *Rivellia pallida* lasted 5–15 minutes; the pre-oviposition period was 7–12 days; and mated females moved down the stem of the plant to deposit eggs in leaf litter and soil. Up to 15 eggs were scattered at each oviposition event and incubation took 6–12 days. Newly hatched larvae entered the soil and moved to the plant root system, where they entered the nitrogen-fixing root nodules. Feeding for 3–5 days, the larvae then exited the nodule through a spherical exit hole and rested for several days prior to entering a fresh nodule. Each larva destroyed between 5 and 10 nodules prior to pupariation at a depth of 5–8 cm in the soil, with a period of 13–21 days prior to eclosion. The life cycle was univoltine.

The eggs and larvae of Platystomatidae are poorly known and immature stages of only a few species have been described. There are larval descriptions for only three species of *Rivellia* and one species each in the non-Afrotropical genera *Duomyia* Walker, *Lenophila* Guérin-Méneville and *Platystoma* Meigen and Afrotropical *Scholastes* Loew (Ferrar 1987: 299). Bibro & Foote (1986) examined the mature larva of *Rivellia pallida*, *R. steyskali* Namba, 1956, *R. viridulans* Robineau-Desvoidy, 1830 and *R. winifredae* Namba, 1956, using scanning electron microscopy, describing and illustrating the first species (Figs 162–164). They concluded that there was little morphological variation in larvae of the four species and that the only character which varied was the number of papillae on the distal margin of the prothoracic spiracle: *Rivellia pallida* (6 or 7), *R. steyskali* (7–9), *R. viridulans* (6 or 7) and *R. winifredae* (9 or 10). Even so, there are unreliable areas of overlap rendering diagnosis difficult.

In general, the egg and third-instar larva can be diagnosed as follows (after Ferrar 1987: 298), but caution should be applied, as these are based on limited information from a few species. The egg measures 0.87–1.4 × 0.3–0.5 mm, is white in colour, cylindrical, straight or slightly curved, with the apex pointed to rounded and tending to be broad (length to width ratio: 2.8 : 1.0) in *Rivellia*, compared to more slender eggs in *Scholastes* (ratio: 6.0 : 1.0). The latter genus exhibits a slight longitudinal groove at the micropylar end.

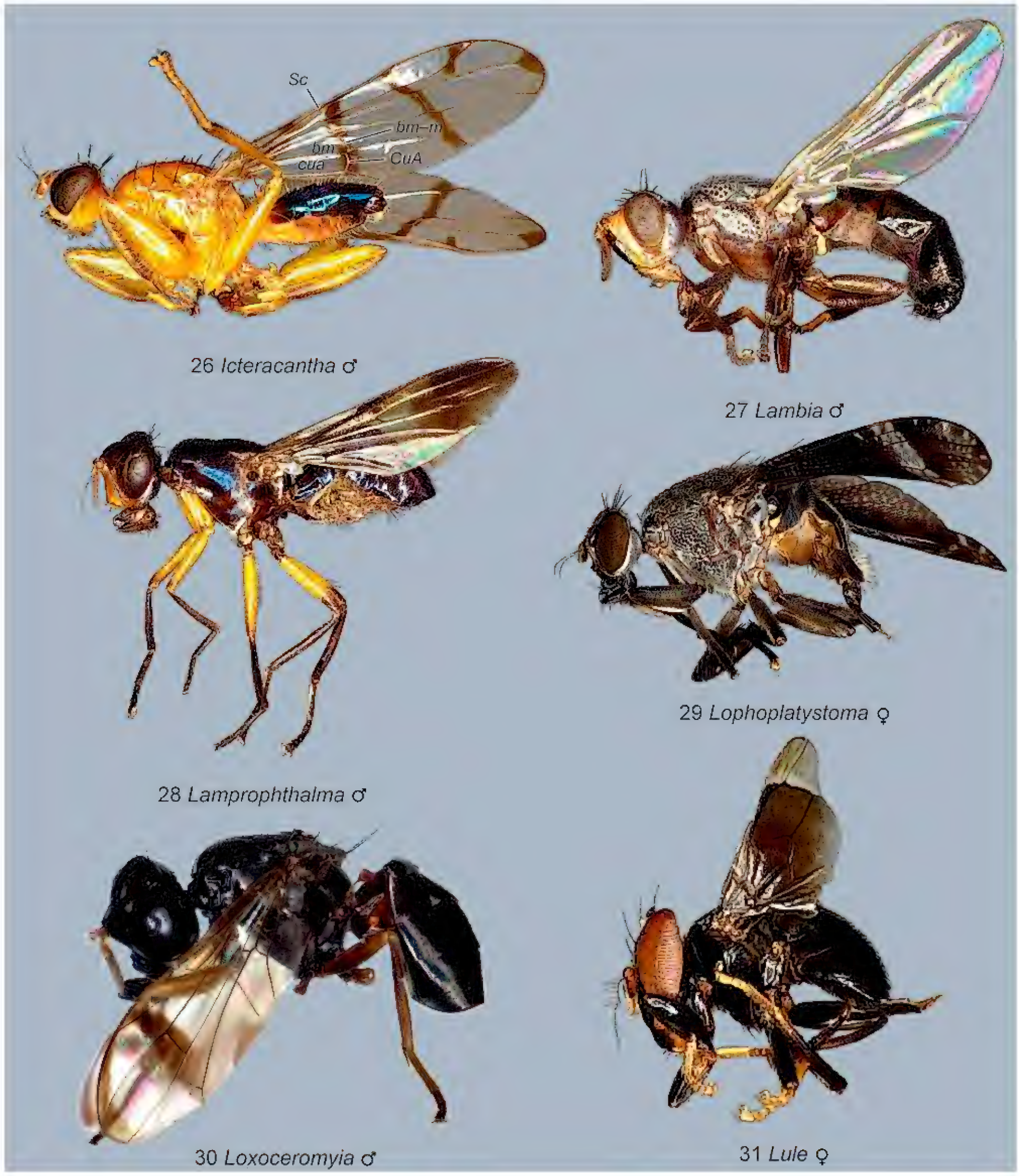
The larva is sub-cylindrical, of the normal schizophoran type and is typical of many Tephritoidea. The first- and second-instar larva were inadequately described by Seeger & Maldague (1960), but measured *ca* 1.0 × 0.23 mm. The third-instar larvae are generally whitish (to slate blue in *Scholastes*), measuring 5.0–16.0 × 1.4–2.0 mm, muscidiform, cylindrical, tapering anteriorly toward the head (Fig. 162). The posterior end is rounded to truncated (Fig. 163) and the body surface is smooth, with spicules only on the ventral creeping welts. The cephaloskeleton (Fig. 165) is variable, according to larval diet, from long, slender, sickle-shaped mouthhooks, without accessory teeth in saprophagous species (*e.g.*, non-Afrotropical *Platystoma euphorbium* Enderlein, 1930), to short squat heavily built mouthhooks, without accessory teeth in phytophagous species (such as *Rivellia* feeding in root nodules of leguminous plants (Whittington 2019)). Furthermore, in the former type a pair of small dental sclerites, a long slender intermediate sclerite and parastomal bar are present and a small dorsal bridge does not connect to either arm; while in the latter type, no dental sclerites are present, the intermediate sclerite is broader and fused to the basal sclerite and both the parasomal bar and dorsal bridge are apparent. The dorsal apodeme of the ventral cornu and the ventral cibarium, illustrated by Hennig (1945) for the saprophagous species, do not appear to be

Figs 70.14–19. Habitus of Platystomatidae (lateral views): (14) *Agrochira corniculata* Whittington ♂; (15) *Atopocnema manicatifrons* Enderlein ♀; (16) *Bromophila caffra* (Macquart) ♂; (17) *Cladoderris convexa* Whittington ♀; (18) *Clitodoca fenestralis* (Macquart) ♂; (19) *Coelocephala arcuata* Bezzi ♂. Fig. 17 (© Trustees of Natural History Museum, London).

Abbreviations: gn – gena; fc – face; fr – frons.

Figs 70.20–25. Habitus of Platystomatidae (lateral views): (20) *Conopariella tibialis* (Hendel) ♀; (21) *Elassogaster* sp. ♂; (22) *Engistoneura moerens* (F.) ♀; (23) *Eudasys ophrys* Whittington ♀; (24) *Federleyella pallidipes* Whittington ♂; (25) *Furcamyia pallida* Whittington ♂. Fig. 23 (© Trustees of Natural History Museum, London).

Abbreviation: gn – gena.



Figs 70.26–31. Habitus of Platystomatidae (lateral views): (26) *Icteracantha femorata* (Macquart) ♂; (27) *Lambia coelocephala* Hendel ♂; (28) *Lamprophthalma ochrifacies* Enderlein ♂; (29) *Lophoplatystoma molle* Hendel ♀; (30) *Loxoceromyia longicornis* Hendel ♂; (31) *Lule corioptera* Speiser ♀. Fig. 30 (© Trustees of Natural History Museum, London).

Abbreviations: *bm* – basal medial cell; *bm–m* – basal medial crossvein; *CuA* – anterior branch of cubital vein; *cua* – anterior cubital cell; *Sc* – subcostal vein.

present in phytophagous species. The prothoracic spiracles are broadly fan-shaped (Fig. 164), with from 6–10 (*Rivellia*) to 12 (*Platystoma*) or 15 (*Lenophila*) papillae, although Bibro & Foote (1986), concluded the number of lobes was not diagnostic. The posterior spiracular plates are sessile (Fig. 163), or at most, on short separate cylindrical tubercles, each plate with three straight, broad and oval spiracular openings set in a radiating pattern (*Platystoma*), or longer and thinner, set almost parallel (*Scholastes*).

The puparium measures 4.8–7.0 × 1.6–2.2 mm, of typical cyclorrhaphous form, being barrel-shaped, tapering abruptly anteriorly and rounded to truncate posteriorly. The ground colour varies from yellow-brown, red-brown and dark brown. No obvious puparial respiratory horns are apparent. The terminal abdominal segment has remnants of five pairs of tubercles in *Duomyia* and the cuticular surface is wrinkled in *Lenophila*.

The biology of the larval stages has been noted for several species over a wide range of resources. The commonest breeding substrate is decaying vegetative matter, but some specialised trends occur in certain genera, *e.g.*, *Rivellia*, which exploits the nitrogen-rich root nodules of legumes (Ferrar 1987: 297; Whittington 2019).

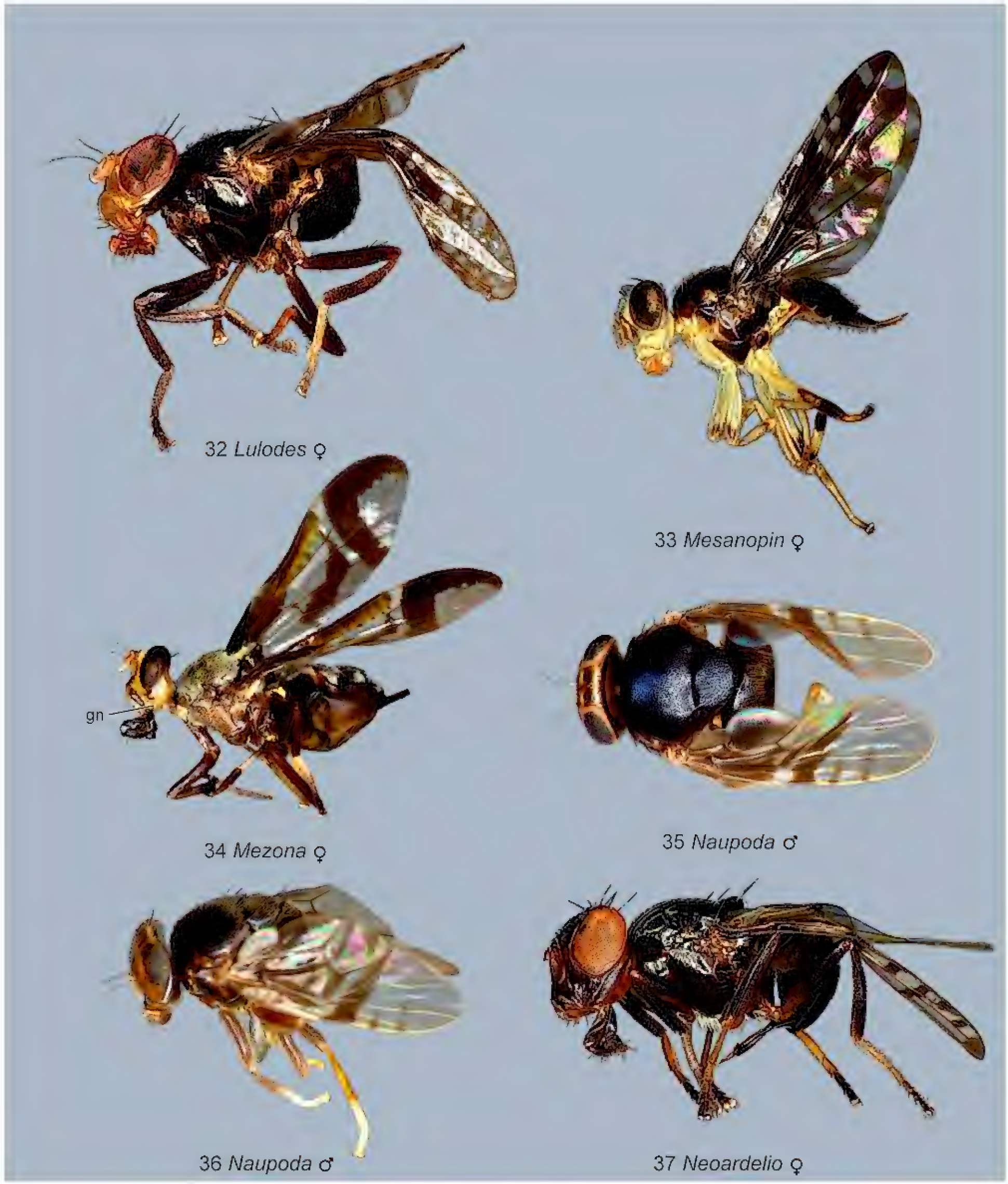
Biological details are known for few Afrotropical species. Frey (1932) recorded *Rivellia granulata* Frey, 1932 and *R. trimucronata* Frey, 1932 on Maize, *Zea mays* L. (Poaceae), at an elevation of 1,000 m. Adults of *Coelocephala arcuata* Bezzi, 1914 (as *C. stigma*) were recorded from chimneys of *Macrotermes natalensis* (Hav.) in Liberia, suggesting a biological association with termites (Steyskal 1965*b*). Some specimens (near *Naupoda nyasica* Frey, 1932) were reared from larvae scavenging in galleries of platypodid beetles, *Trachyostus schaufussi* Schedl (Curculionidae) in logs of *Celtis mildbraedii* Engl. (Cannabaceae) in lowland rainforest in Nigeria (Roberts 1969). *Neoardelio aspalathus* Whittington, 2000 and *N. lineatocollis* (Thomson, 1869) are both possibly associated with the root nodules of the Rooibos tea plant, *Aspalathus linearis* (Burman f.) Dahlgren (Fabaceae) (Whittington 2000*b*). Male and female specimens of *Parardelio* Hendel species were observed resting on bananas in Madagascar (Whittington 2009: 311) and *Plastotephritis patagiata* Enderlein, 1922, has been collected from *Macaranga hirifolia* Thou. (Euphorbiaceae) (Whittington 2003).

In the Australasian Region, McAlpine (1973*a*) recorded *Duomyia* reared from puparia occurring in sand and from Mandarin orange (*Citrus reticulata* Blanco) (Rutaceae). Larvae of *Elassogaster linearis* (Walker, 1849) (as *E. sepsoides*) were reported consuming the egg pods of *Locusta migratoria* (L.) (Acrididae) by Greathead (1963) and in rotting vegetation (taro roots and asparagus crowns) by McAlpine (2001). *Euprosopia megastigma* McAlpine, 1973, was recorded consuming the larvae of an unidentified scarabaeine beetle and *E. tenuicornis* Macquart, 1847 and *Lenophila dentipes* (Macquart, 1843) were observed to oviposit in sap exuding from beetle damage to a *Eucalyptus* tree (McAlpine & Kim 1977). McAlpine & Kim (1977) reported three other species of *Lenophila* (*L. achilles* McAlpine & Kim, 1977, *L. coerulea* (Macquart, 1846) and *L. secta* McAlpine & Kim, 1977), reared from rotting trunks of the Grass tree, *Xanthorrhoea* (Xanthorrhoeaceae). A specimen of *Pogonortalis dolcea* (Walker, 1849) was reared from freshly dug soil (McAlpine 1973*a*) and McAlpine (2001) reported an association between adult *Rivellia* and *Acacia* (Fabaceae) in Australia. Diatloff (1965) recorded the larvae of an unidentified species in active and decayed root nodules of *Glycine javanica* L. (Fabaceae), a pasture legume in south-east Queensland, evidently attacking functional nodules and causing these to decay, posing a potential economic loss. In Guam Is. in the Pacific, larvae of *Scholastes aitapensis* Malloch, 1939 occurred in rotting coconuts and adults were collected from carrion, dung and rotting papayas (Bohart & Gressitt 1951); while *S. bimaculatus* Hendel, 1914 was reared from (McAlpine 1973*a*) and *S. lonchifer* Hendel, 1914 was found ovipositing into, ripe coconuts (Aubertin & Cheeseman 1929). In an unpublished study of succession on carrion, a *Pogonortalis* Hendel species and *Euprosopia comes* McAlpine, 1973 were recorded in the bloat stage of decomposition (J. Farrell & A.E. Whittington, pers. obs.).

Biological details from the Palaearctic Region are few and are restricted to the genera *Platystoma* and *Rivellia*. Hennig (1945) recorded the larvae of *P. euphorbiinum* Enderlein, 1930, from rotting roots of *Euphorbia canariensis* L. (Euphorbiaceae) in the Canary Is.; larvae of *P. lugubre* (Robineau-Desvoidy, 1830) were recorded from soil beneath a fallen tree in Europe; and adults of *P. seminationis* (F., 1775) from sap runs on oak and elm in Japan. Hennig (1952: 198) further recorded large numbers of *P. lugubre* in a German cemetery, where wartime bombing victims were buried without coffins. Korneyev *et al.* (2015) reported larvae of *Platystoma rufipes* (Meigen, 1826) inhabiting the stems of *Crambe* (Brassicaceae), infested by a Lixini weevil larvae, where the signal fly larva was feeding on a rotting mix of plant remnants and weevil larval frass or possibly on the dead grubs themselves. This type of feeding is believed to be universal for most non-phytophagous Tephritoidea families, including Lonchaeidae, Pallopteridae, Richardiidae, Tephritidae (Acanthonevrini and Gastrozonini) and Ulidiidae (Lipsanini and Ulidiini) (V. Korneyev, pers. comm. 2020).

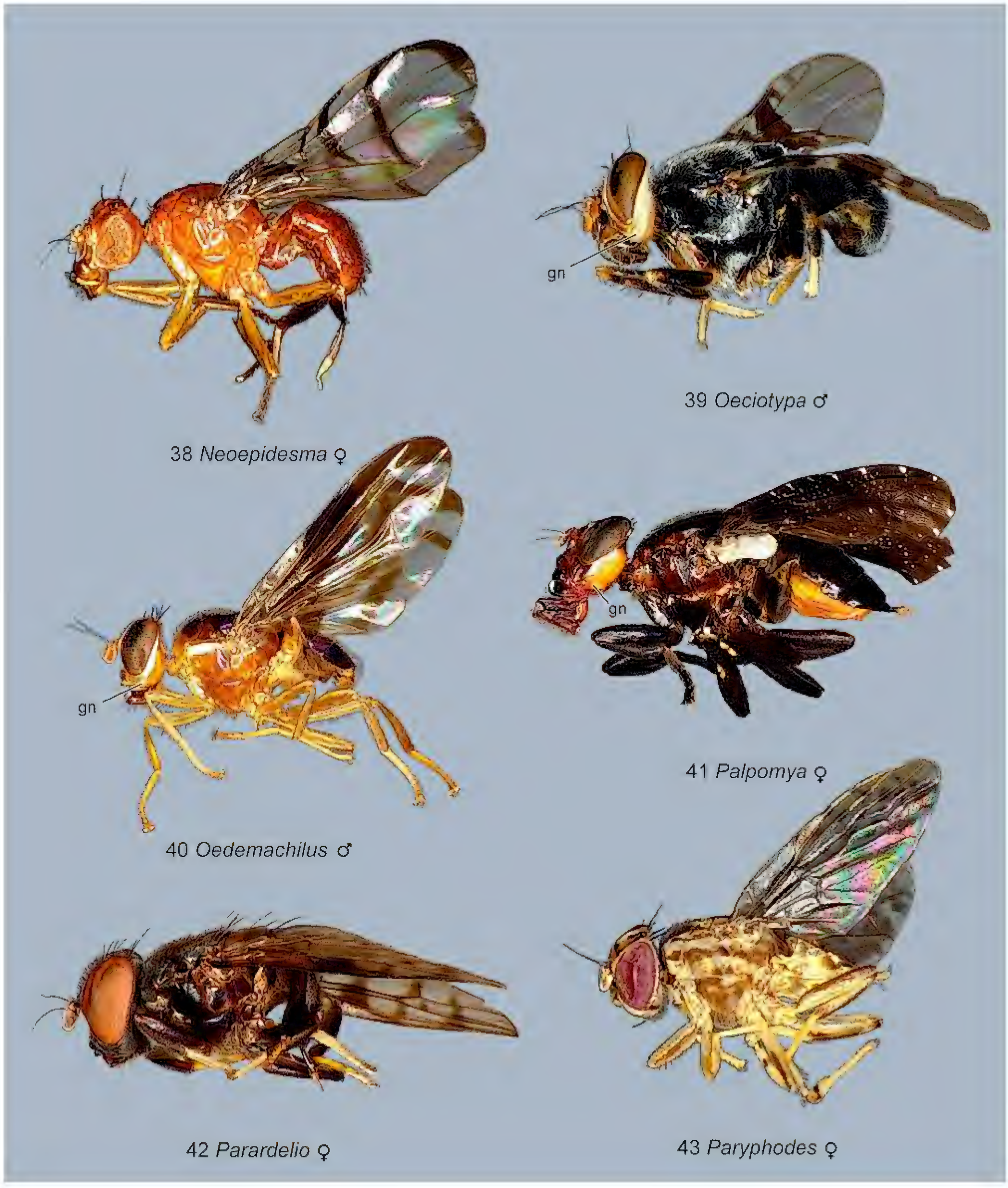
Likewise, almost nothing is known for species occurring in the Oriental Region; the only accounts being for *Poecilotraphera comperei* (Cocquillett, 1904), *P. diaereta* Steyskal, 1965 and *P. taeniata* (Macquart, 1843), respectively, reared from Guava, *Psidium guajava* L. (Myrtaceae) in India, from tunnels in Maize, in Assam, India and dead Winter rice, *Oryza sativa* L. (Poaceae) in West Bengal and lastly feeding on dead larvae of Rice-borer, *Chilo polychrysus* (Meyrick) (Crambidae) in Bangladesh and Thailand (Steyskal 1965*c*). A similar niche is utilised by the larvae of many Oriental Gastrozonini (Tephritidae: Dacinae) and Neotropical Lipsanini (Ulidiidae), that often feed in tall grasses (bamboos, Maize, *etc.*), having saprophagous or rarely, phytophagous larvae (V. Korneyev, pers. comm. 2020). Females of most species of the aforementioned tribes that oviposit deep into tight axils of bamboos, have the aculeus of the ovipositor flattened and the cercus flat, apically sharpened and hardened (V. Korneyev, pers. comm. 2020), similar to many Plastotephritinae genera of Platystomatidae, which possibly have similar adaptation for oviposition into narrow, tight crevices, although perhaps in different plants.

In the Nearctic Region, besides the studies on *Rivellia*, *Amphicnephes pullus* (Wiedemann, 1830), is known from rotting Daffodil, *Narcissus pseudonarcissus* L. (Amaryllidaceae) bulbs (Blanton 1938). Courtship behaviour was first discussed by Piersol (1907), for *R. boscii* Robineau-Desvoidy, 1830 and the



Figs 70.32–37. Habitus of Platystomatidae: (32) *Lulodes seriatopunctatus* Enderlein, lateral view ♀; (33) same, *Mesanopin tridens* Whittington ♀; (34) same, *Mezona proxenus* Speiser ♀; (35) *Naupoda inscripta* Speiser, dorsal view ♂; (36) same, dorsolateral view; (37) *Neoardelio longiala* Steyskal, lateral view ♀.

Abbreviation: gn – gena.



Figs 70.38–43. Habitus of Platystomatidae (lateral views): (38) *Neoepidesma thoracale* Hendel ♀; (39) *Oeciotypa hendeli* Lindner ♂; (40) *Oedemachilus coquereli* Bigot ♂; (41) *Palpomya asphaltina* (Wiedemann) ♀; (42) *Parardelio voeltzkowi* Enderlein ♀; (43) *Paryphodes duus* Steyskal ♀.

Abbreviation: gn – gena.

biology and larval feeding habits of *R. pallida* were discussed by Bibro & Foote (1986) and Foote (1985). Foote (1985) also listed the host-plants of eight of the 34 Nearctic *Rivellia* species occurring in the region. *Rivellia micans* Loew, 1873 and *R. munda* Namba, 1956, were recorded on the host-plant False indigo, *Amorpha fruiticosa* L. (Fabaceae) by Foote *et al*. (1987) and McMichael *at al*. (1990) provided a detailed account of the biology and life cycle of *R. melliginis* (Fitch, 1855), illustrating and tabulating elements of courtship behaviour.

Economic significance

As noted in the section on Biology and immature stages above, there are instances of larval associations either with root nodules or with stems and fruits of numerous crops. Most of these are unevaluated as far as economic importance is concerned. *Rivellia* (Figs 12, 52) is the only genus for which detailed studies of the economic biology of the larval stages have been published. Larvae are associated with the living and decaying root nodules of nitrogen-fixing Fabaceae and with the roots or flowers of other plants, many of which are important agricultural crops (Whittington 2019), predominantly consisting of various types of pea and bean, such as Soya and Mung bean, Pigeon-pea, Groundnut, *etc*. The growing economic importance associated with this biology hinges on increased demands for legume crops, especially Soybean, *Glycine max* (L) Merrill. This crop is not only used in human food supply, but also as stock feed that indirectly benefits the human food chain. At least 22 species of *Rivellia* are associated with root nodules of legumes. Whittington (2019) listed 32 different plant species interactions with many more varieties among these. At least seven species of *Rivellia* impact on the Soybean trade, which amounts to a global production of nearly 350 million tonnes per annum (FAO 2017). This accounts for 56% of global oilseed production, with a market value of in excess of USD48 billion (Wilson 2008: 3). So significant is the pest association of the non-Afrotropical species, *R. quadrifasciata* (Macquart, 1835), that it has become known as the Soybean nodule fly (Koethe & van Duyn 1984). In the USA, Foote *et al*. (1987) suggested that *Rivellia* species associated with root nodules of legume crops have shifted from a primary indigenous meadow legume to the mono-cultured crop species.

In the Afrotropical context, the only report is for an undetermined *Rivellia* species from Yangambi in Democratic Republic of the Congo (Seeger & Maldague 1960), where larvae were found to occur on root nodules of Peanut, Mung bean, Cowpea, Bambara groundnut, *Voandzeia subterraneana* (L.) Verdc., but not on Soybean and *Crotalaria longithyrsa* Baker f. in the same trials.

Classification

The first described species of Platystomatidae were placed in the large family Muscidae, where they often appeared listed in the subfamilies Achiides, Ortalides or Sepsides (e.g., Walker 1858) and Anthomyzidae (Doleschall 1858). Other early authors, such as Wulp (1896), used the more familiar subfamily suffix and recognised a distinction between Ortalinae and Trypetinae. Later, F. Hendel's significant contribution and reorganisation of the world genera (Hendel 1914*a*, *b*), firmly placed the Platystomatidae as a subfamily of Muscaridae, divided into several tribes that are seldom applied today.

The oldest family-group name is not Platystomatidae, but Achiasidae Fleming (described in 1821) and based on the genus *Achias* F., 1805. There has, however, been an overwhelming predominance of the usage of names based on the genus *Platystoma*. The name Platystominae was first proposed by Schiner (1862) and upon petition by Steyskal & McAlpine (1974), the International Commission on Zoological Nomenclature (1979) ruled under plenary power that family-group names based on *Achias* should be suppressed, giving those based on *Platystoma* precedence.

Species now assigned to Platystomatidae have previously been placed either as a family or a subfamily in the Otitidae (= Ulidiidae) as Platystomidae or Platystominae (e.g., Hendel 1912; Hennig 1941; Lamb 1914), or as Platystomatidae or Platystomatinae (Steyskal & McAlpine 1974). Alternative placements include: Ortalidae (Bezzi 1908, 1914, 1918; Curran 1928; Enderlein 1912; Frey 1930; Speiser 1910, 1914, 1915), Ortalinae (e.g., de Meijere 1911, 1913, 1919), Phytalmiidae (e.g., Steyskal 1950) and Trypetidae (Loew 1861).

Frey (1932), recognising the group as Platystomidae, applied subfamilial divisions based on Hendel's (1914*a*) and Enderlein's (1922) tribal names. Despite this, Steyskal (1960) used the tribal names in the subfamily Platystominae in the family Otitidae. Later, Hennig (1958), followed by Steyskal (1961), clearly separated the Ulidiidae (as Otitidae) and Platystomatidae, with substantial character synapomorphies within the Otitoidea, suggesting that these families were not only interrelated, but formed distinct lineages, after which Steyskal assigned the now well-established subfamily status. These were followed and refined by McAlpine (1973*a*, 1982: 662, 2001). From this springboard has developed the modern approach to the position of this family within the Tephritoidea and the definitions of the subfamilies comprising it.

Contrary to this approach, Griffiths (1972: 253) subordinated all the Tephritoidea into Tephritidae *sensu lato* on the grounds that he did not assess the radiation of families within this family to be of equivalent age to families in the remainder of the Schizophora. In more modern treatments there has been considerable rearrangement of the families. McAlpine (1989) shifted Griffith's concept upwards to superfamily level, thereby reinstating the subgroups to family-level. As a result, Platystomatidae were placed in sister-group context by McAlpine (1989: 1440) with Tephritidae + Pyrgotidae + Tachiniscidae, remaining more generalised and closer to the groundplan than the other three families, which were really only distinguishable by the acute posteroapical lobe to wing cell *cua*.

Platystomatidae were included in the monophyletic cluster termed "higher Tephritoidea" by Korneyev (1999: 10), along with Ulidiidae (= Otitidae and = Pterocallidae), Pyrgotidae and Tephritidae (including Tachiniscidae), with the last two named families being the sister-group to the Platystomatidae. Subsequently, Han & Ro (2005) analysed mitochondrial 12S, 16S and COII genes within the Tephritoidea, concluding that the molecular evidence only weakly supported the conclusions of the earlier morphological phylogenies of McAlpine (1989) and Korneyev (1999), with mixed results for the maximum

Figs 70.44–49. Habitus of Platystomatidae (lateral views): (44) *Peltacanthina* sp. ♀; (45) *Phlebophis serpentina* Frey ♀; (46) *Phytalmodes africanus* Bezzi ♀; (47) *Plagiostenopterina* sp. ♂; (48) *Plastotephritis sica* Whittington ♀; (49) *Pseudepicausta* sp. ♂. Fig. 48 (© Trustees of Natural History Museum, London).

Abbreviations: gn – gena; fc – face; fr – frons.

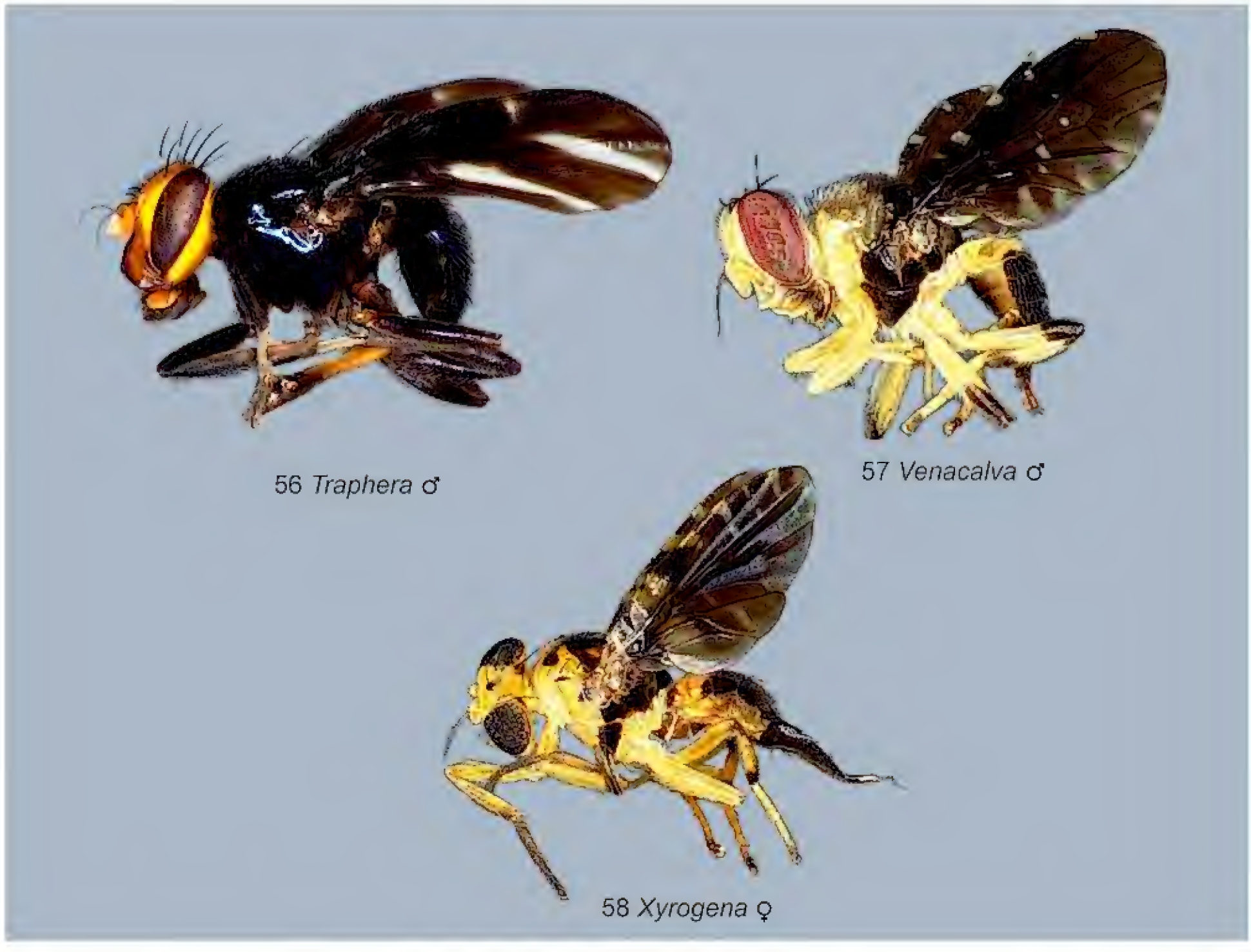
Figs 70.50–55. Habitus of Platystomatidae (lateral views): (50) *Pseudoscholastes marshalli* Frey ♀; (51) *Pterogenomyia picta* (Bigot) ♀; (52) *Rivellia* sp. ♂; (53) *Scholastes vicarius* Hendel ♀; (54) *Seguyopiara* sp. ♀; (55) *Sphenoprosopa fascipennis* Macquart ♂. Fig. 51 (© Royal Museum for Central Africa).

Abbreviations: gn – gena; fc – face; fr – frons.

likelihood (ML), maximum parsimony (MP) and minimum-evolution (ME) trees. Consequently, the authors concluded that Tephritoidea may not be monophyletic, or that it is monophyletic, but with low phylogenetic signal. Nonetheless, the ME tree resulted in two monophyletic subgroups, one supporting a sister-group relationship between Piophilidae + Lonchaeidae + Pallopteridae (that is Pallopteroidea *sensu* Hennig 1958) and the other supporting Ulidiidae + Platystomatidae + Tephritidae + Pyrgotidae + Richardiidae (that is Otitoidea *sensu* Hennig 1958). The important conclusion of this study regarding the Platystomatidae, is that while it is clearly considered monophyletic from a morphological (Korneyev 1999; McAlpine 1989) and molecular (Han & Ro 2005) perspective (ML and MP trees), it is weakly supported by the ME tree and that Platystomatidae may be a paraphyletic group early branching to the Ulidiidae. This contradiction focusses on the need for further phylogenetic work in the Tephritoidea as a whole and within Platystomatidae at the subfamily and generic levels.

The most complete phylogeny of Diptera to date (Wiegmann *et al*. 2011), concluded that the Tephritoidea diversified about 75 MYA, while Han & Ro (2016) determined that Platystomatidae diversified at 40 MYA. The molecular phylogenetic analysis of Wiegmann *et al*. (2011) is not consistent with the conclusions of previous morphological (Korneyev 1999; McAlpine 1989) and molecular (Han & Ro 2005) studies. Instead, the early branching Richardiidae + Lonchaeidae lineage is distinct from the remaining families, consisting of Piophilidae + Ulidiidae + Platystomatidae + Ctenostylidae + Tephritidae + Pyrgotidae + Tachiniscidae. The most recent study (Han & Ro 2016) indicated that the Tephritidae family group (approximately the "higher Tephritoidea" *sensu* Korneyev 1999: 10), is supported by 12S, 16S, COI and COII gene sequences.

The most significant modern publication dealing with the family status and characterisation of the Platystomatidae was McAlpine's (1973*a*) revision of the Australasian representatives, followed by a review of the Australasian genera (McAlpine 2001). He provided good characters and reasoning for family status of the Platystomatidae, separate from the Tephritidae and other tephritoid families and clearly defined and delimited five subfamilies.

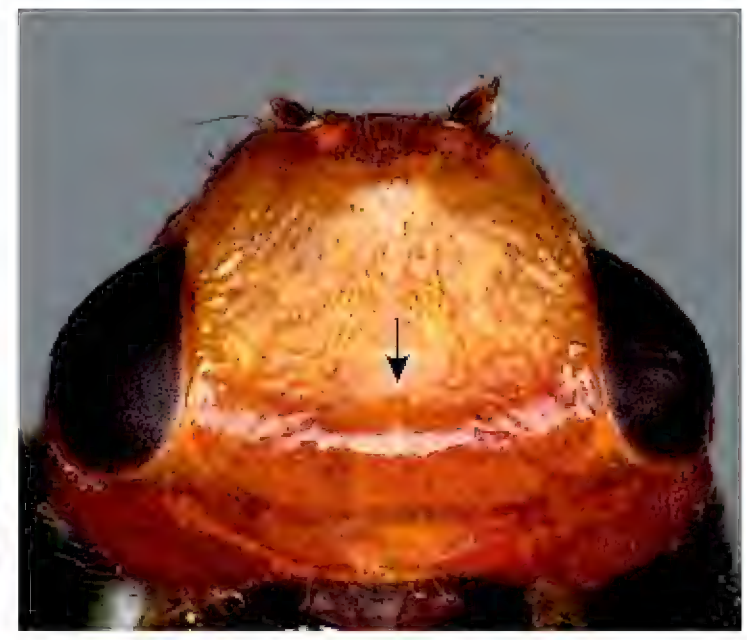


Figs 70.56–58. Habitus of Platystomatidae (lateral views): (56) *Traphera chalybea* Wiedemann ♂; (57) *Venacalva virga* Whittington ♂; (58) *Xyrogena gratiosa* (Enderlein) ♀.

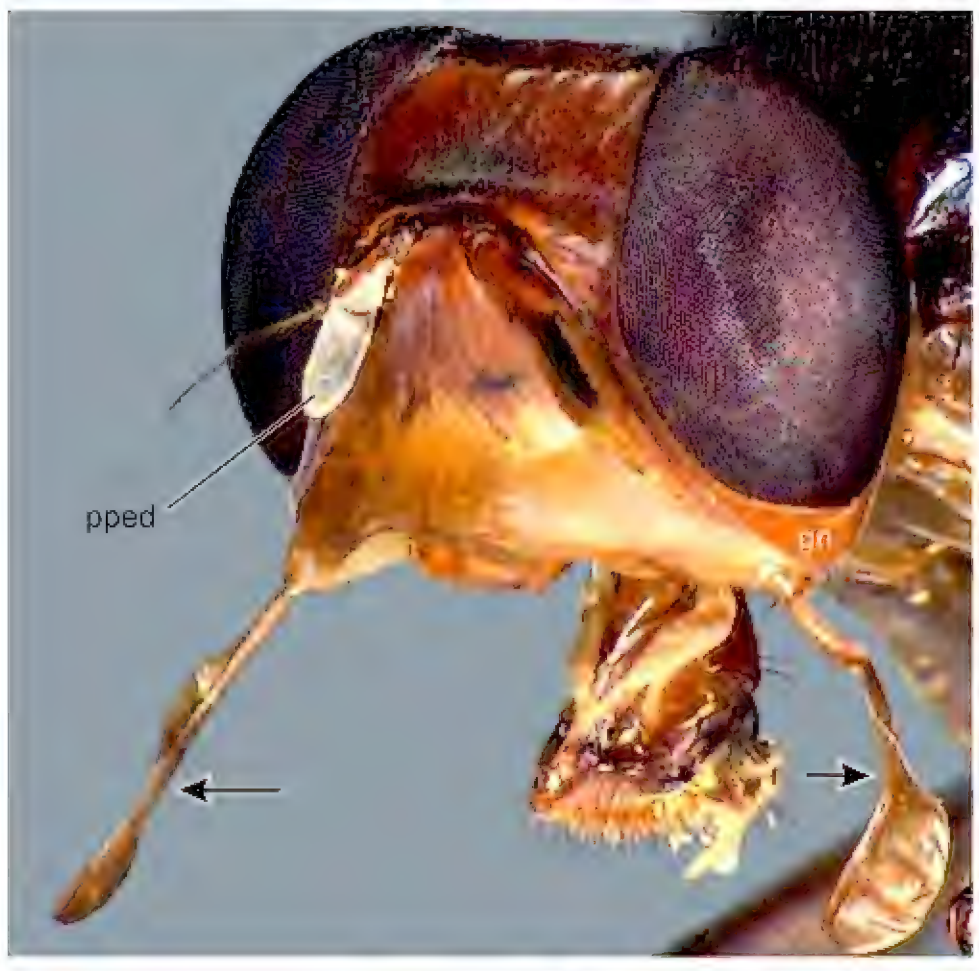
McAlpine (2001) revised the number of subfamilies to four, incorporating Angitulinae into Platystomatinae. The remaining three subfamilies being: Plastotephritinae, Scholastinae and Trapherinae. A full phylogenetic analysis of the family is required, however, to elucidate subfamily distinctions and for present, subfamilies should perhaps be viewed as a guide only. Placement of some genera within subfamilies has proven problematic, as demonstrated by the recent repositioning of Australasian genera previously placed in Angitulinae, together with uncertainties concerning the monophyletic status of Scholastinae (McAlpine 2001) and the assignment of certain non-Afrotropical genera, e.g., *Apiola* McAlpine, *Atopognathus* Bigot, *Chaetorivellia* de Meijere, *Guamomyia* Malloch (McAlpine 2001) and Afrotropical *Piara* Loew.

Similar uncertainties remain within the Afrotropical fauna. For example, the lower calypter reduced to a narrow linear fringe (Fig. 89) was considered a useful character for separating specimens of Plastotephritinae (Whittington 2000*a*, *b*, 2003), but is also apparent in some genera of Platystomatinae (*i*.e., *Clitodoca* Loew (Fig. 90), *Icteracantha* Hendel, *Phlebophis* Frey and *Phytalmodes* Bezzi). In these genera it appears that both calypters are equally vestigial, while in Plastotephritinae, the upper calypter is often developed, while the lower one is not.

59 *Agrochira* ♂



60 *Bromophila* ♀



61 *Clitodoca* ♂

62 *Coelocephala* ♂

Figs 70.59–62. Heads of Platystomatidae: (59) *Agrochira corniculata* Whittington, dorsal view ♂; (60) same, *Bromophila caffra* (Macquart) ♀ (arrow indicates absence of ocelli); (61) *Clitodoca fenestralis* (Macquart), oblique frontal view ♂ (arrows indicate spatulate extensions of genae); (62) *Coelocephala arcuata* Bezzi, frontal view ♂.

Abbreviations: gn – gena; pped – postpedicel; vrt – vertex.

Another character used by Whittington (2003) to define the Plastotephritinae was the subcostal wing vein (*Sc*) ending before reaching the costal vein (*C*) (Fig. 139). On closer examination of *Clitodoca* (Fig. 140), *Phlebophis* and *Phytalmodes* (Fig. 141), it is clear that these genera (at present assigned to the Platystomatinae), share this character with the Plastotephritinae, rather than the alternative state common to Platystomatinae that the subcostal wing vein ends at the costal vein (Figs 142, 143). In the genus *Traphera* Loew (Trapherinae), the subcostal vein appears not to join the costal vein, ending abruptly

63 *Conopariella* ♂

64 *Conopariella* ♂

65 *Engistoneura* ♀

66 *Mezona* ♀

Figs 70.63–66. Heads of Platystomatidae: (63) *Conopariella tibialis* (Hendel), lateral view ♂; (64) same, frontal view; (65) *Engistoneura moerens* (F.), frontal view ♀ (arrow indicates broad upper facial carina); (66) same, *Mezona proxenus* Speiser ♀ (arrow indicates narrow upper facial carina).

Abbreviations: gn – gena; i vt s – inner vertical seta; o vt s – outer vertical seta; pped – postpedicel.

67 *Lamprophthalma* ♂

68 *Scholastes* ♂

69 *Eudasys* ♀

70 *Parardelio* ♀

Figs 70.67–70. Heads of Platystomatidae: (67) *Lamprophthalma rufoscutellata* Hendel, oblique frontal view ♂; (68) same, *Scholastes vicarius* Hendel ♂; (69) *Eudasys ophrys* Whittington, frontal view ♀; (70) same, *Parardelio voeltzkowi* Enderlein. Fig. 69 (© Trustees of Natural History Museum, London).

Abbreviations: fr – frons; oc – ocelli; pped – postpedicel; trn rg – transverse ridge.

but in contact with it (Fig. 144). The question of characterisation of the subfamilies as suggested by McAlpine (2001) for the Australasian fauna is confirmed for the Afrotropical fauna, clearly requiring detailed phylogenetic analysis before it can be fully resolved.

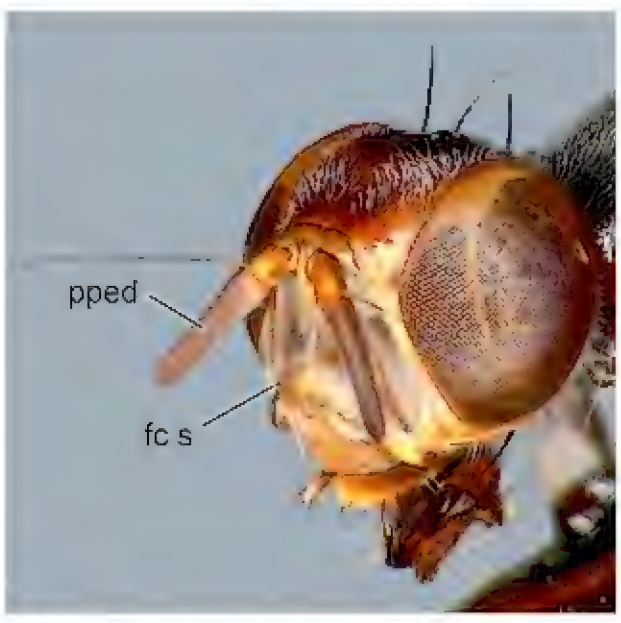
Another issue requiring further investigation, is the highly modified wing venation shared by *Lulodes* (Platystomatinae) and representatives of the subfamily Scholastinae (*Naupoda* and in Australasia: *Asyntona* Osten Sacken, *Naupoda* (subgenus *Gonga* McAlpine) and *Mesoctenia* Enderlein) and with the trapherine genera *Lule* and *Phylax* McAlpine (Australasian). Cell *bm* of the wing is triangular to kite-shaped, considerably wider at the apex than at the base; cell *br* is narrow and distorted, cell *dm* is large, rectangular and virtually parallel-sided (Figs 109, 110, 114). As a result of the considerable widening of cells *bm*, *cua* and *dm*, the cells *c*, *sc*, base of r_1 and *br* are constricted toward the costal vein (*C*), with the consequence that crossvein *r–m* is markedly shorter than crossvein *bm–m*.

McAlpine (1973*a*, 2001) considered the presence or absence of the katepisternal setae (Fig. 85) to be of doubtful value at the subfamilial-level, although for the Afrotropical fauna it is a useful character to distinguish Plastotephritinae and Platystomatinae from Scholastinae and Trapherinae. There is still room for debate regarding the paraphyletic nature of at least Scholastinae (McAlpine 2001) and Trapherinae. McAlpine (2001) further pointed out that delimitation of the subfamilies is problematic, so it is clear that a full phylogenetic analysis of the family is required to evaluate subfamily relationships.

Plastotephritinae (Figs 3, 7) is a small subfamily, with 90 species globally (Whittington 2003). The Afrotropical fauna was

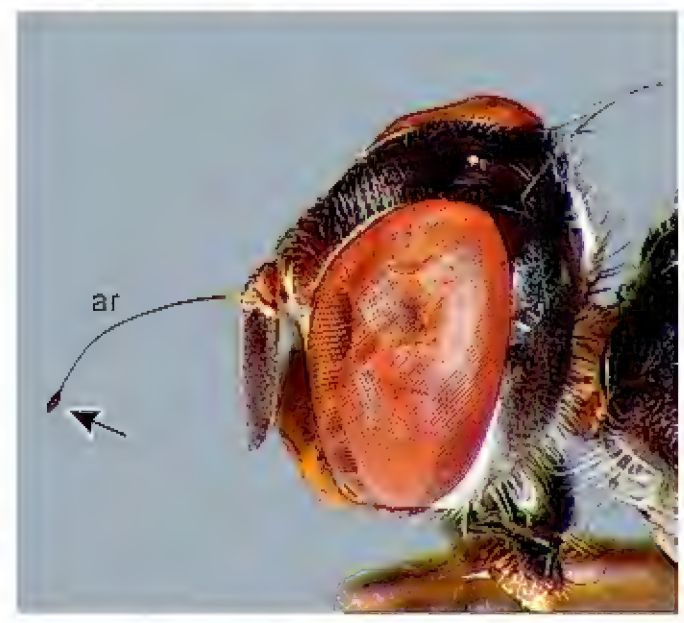
71 *Paryphodes* ♀

72 *Phytalmodes* ♀



73 *Plagiostenopterina* ♂

74 *Plagiostenopterina* ♀

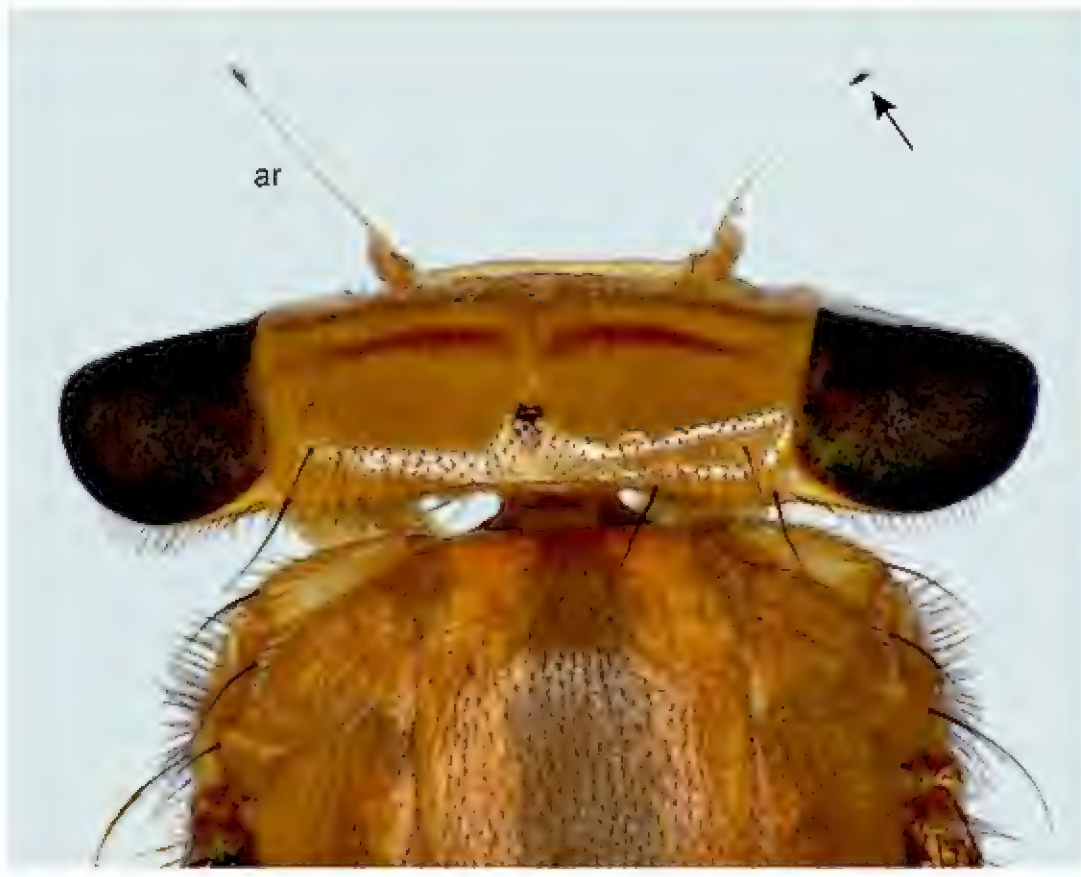


75 *Plagiostenopterina* ♂

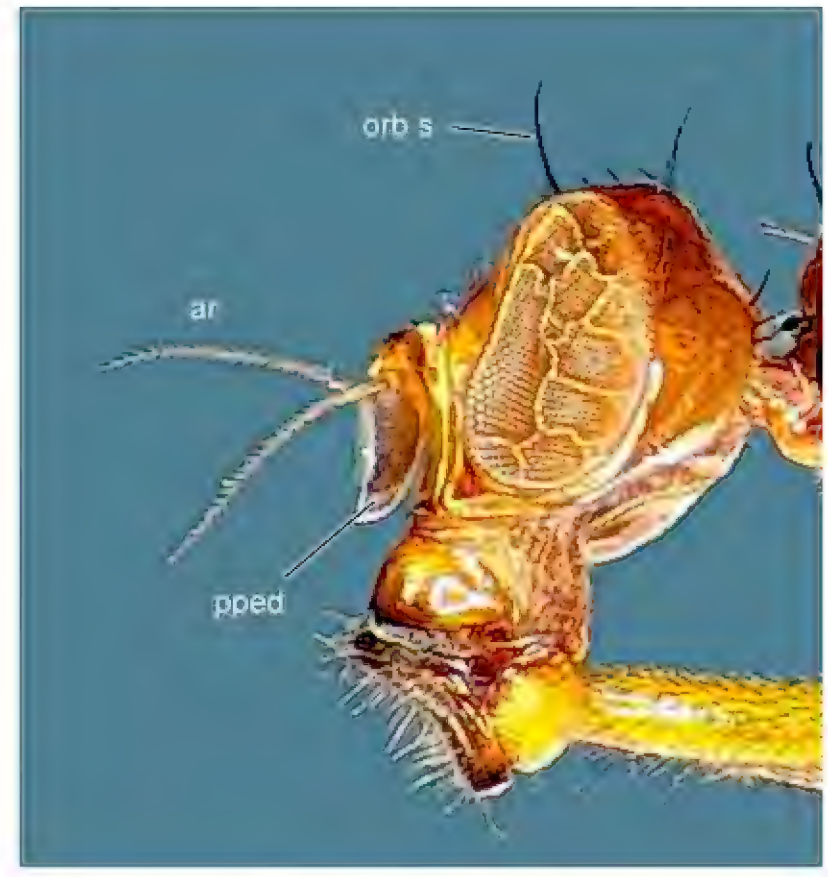
Figs 70.71–75. Heads of Platystomatidae: (71) *Paryphodes nepticula* (Loew), frontal view ♀; (72) same, *Phytalmodes africanus* Bezzi ♀; (73) *Plagiostenopterina* sp., oblique frontal view ♂; (74) same, dorsal view ♀; (75) *Pl. submetallica* (Loew), oblique lateral view ♂ (arrow indicates spatulate apex of arista).

Abbreviations: ar – arista; fc s – facial setae; fr – frons; gn – gena; l pocl s – lateral postocular seta; pped – postpedicel.

revised by Whittington (2003) and now comprises 16 genera, with 78 species. The majority of species occur in the Afrotropics, with two genera and three species recorded from the Oriental Region. The fauna of the Australasian/Oceanian Region awaits revision, but will likely account for fewer species (*ca* 10, Whittington 2003) than occur in the Afrotropics. The subfamily is absent from the Palaearctic Region, the New World and Antarctica. Distinguishing features include the following: head to some extent compressed, appearing narrow in lateral view (Fig. 63); the katepisternal setae are invariably absent; the subcostal wing vein (*Sc*) ends abruptly (Fig. 139), or is angled forward toward the costal vein (*C*) and is evanescent; the lower calypter is reduced to a narrow, linear fringe (Fig. 89), while the upper calypter is present, albeit narrowly so; the male phallus

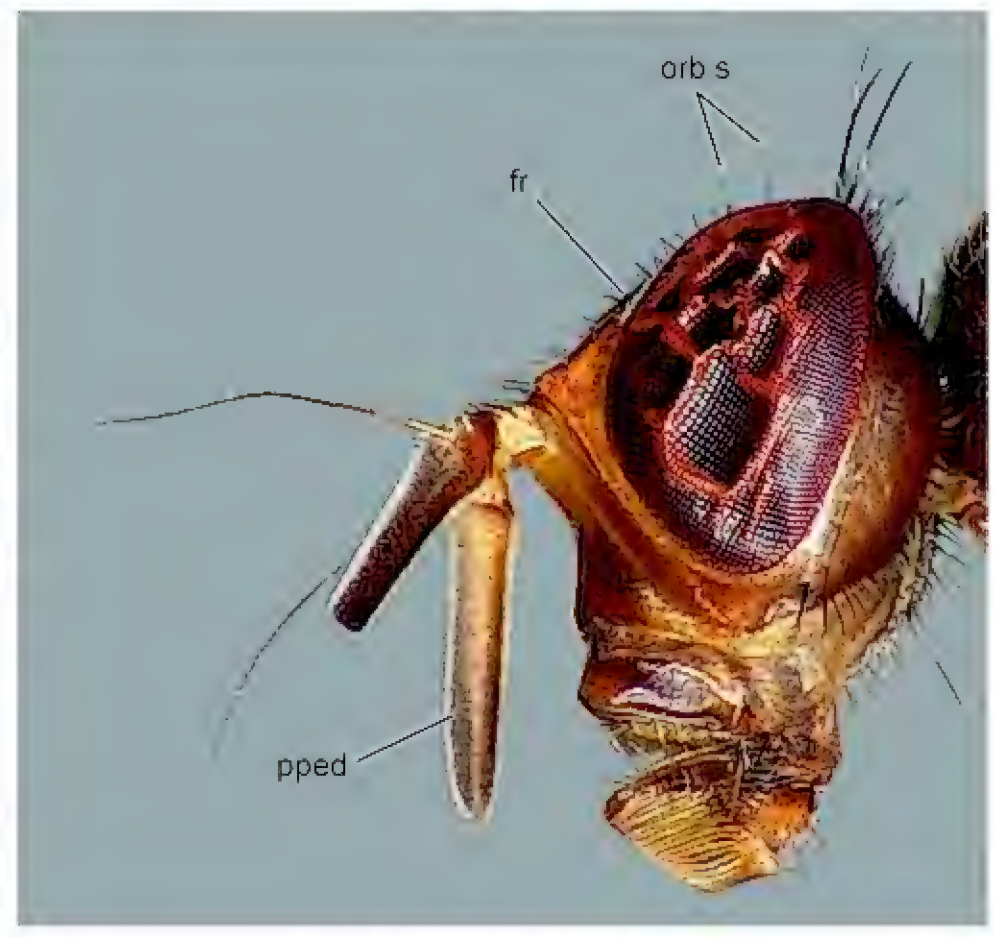


76 *Pseudoscholastes* ♀



77 *Neoepidesma* ♀

78 *Parardelio* ♀



79 *Pseudepicausta* ♀

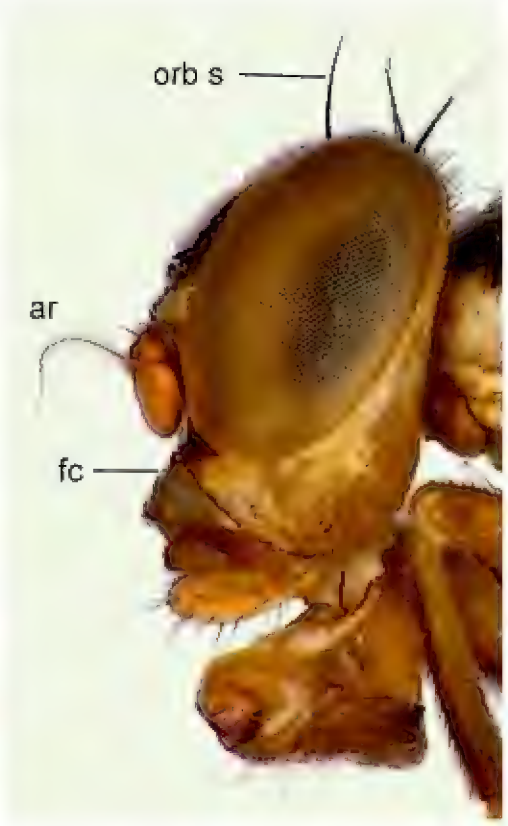
Figs 70.76–79. Heads of Platystomatidae: (76) *Pseudoscholastes marshalli* Frey, dorsal view ♀ (arrow indicates spatulate apex of arista); (77) *Neoepidesma thoracale* Hendel, lateral view ♀; (78) same, *Parardelio voeltzkowi* Enderlein ♀; (79) same, *Pseudepicausta* sp. ♀.

Abbreviations: ar – arista; fr – frons; pped – postpedicel; orb s – orbital seta(e).

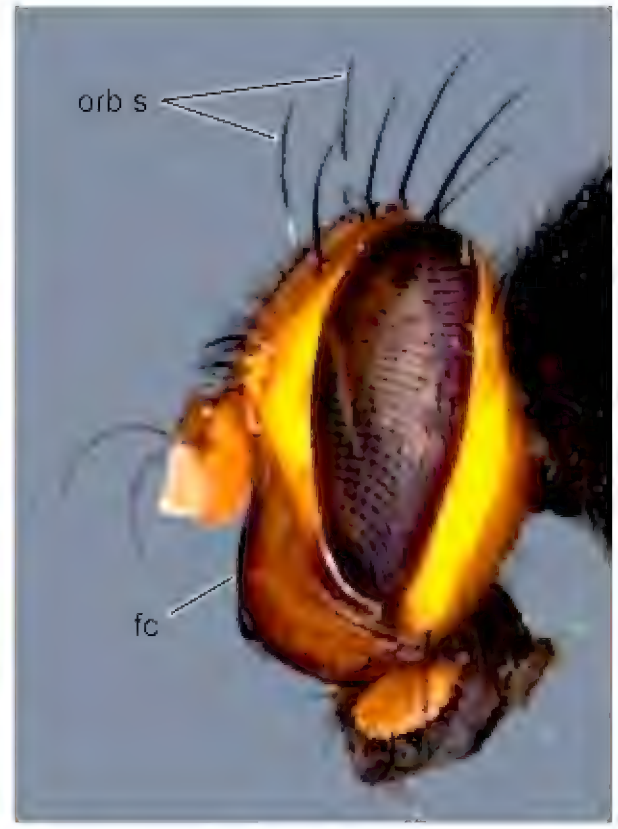
terminates in a glans, without terminal filaments; tergite 6 in the female is vestigial to absent; and the female aculeus is variable, often broad with an acute apex (Figs 157, 159–161). These characters are useful in combination, but individual characters are shared with representatives of other subfamilies. Whittington (2003) proposed two tribal subdivisions for the subfamily: Agrochirini (further divided into the *Agrochira* genus-group and the *Cladoderris* genus-group) and the Plastotephritini. Sexual dimorphism is common (Whittington 2006), with males having modified fore femora and various extensions to the head (Whittington 2003), all of which are integral to agonistic behaviour, as demonstrated for species in other subfamilies by McAlpine (1973*b*, 1975, 1979: 221, 1982: 665). The following Afrotropical genera are included in the subfamily: *Agrochira* Enderlein; *Atopocnema* Enderlein; *Cladoderris* Bezzi; *Conopariella* Enderlein; *Eudasys* Whittington; *Federleyella* Frey; *Furcamyia* Whittington; *Mesanopin* Enderlein; *Micronesomyia* Whittington; *Oeciotypa* Hendel; *Plastotephritis* Enderlein; *Prosopoconus* Enderlein; *Pterogenomyia* Hendel; *Stellapteryx* Whittington; *Venacalva* Whittington; and *Xyrogena* Whittington.

Platystomatinae (Figs 1, 2, 4, 5, 8–12) is the largest subfamily, with an estimated *ca* 900 species globally (Whittington unpubl.). The Afrotropical fauna comprises 26 genera, with *ca* 160 species (including some undescribed species). A few selected Afrotropical genera have been revised, but for the most

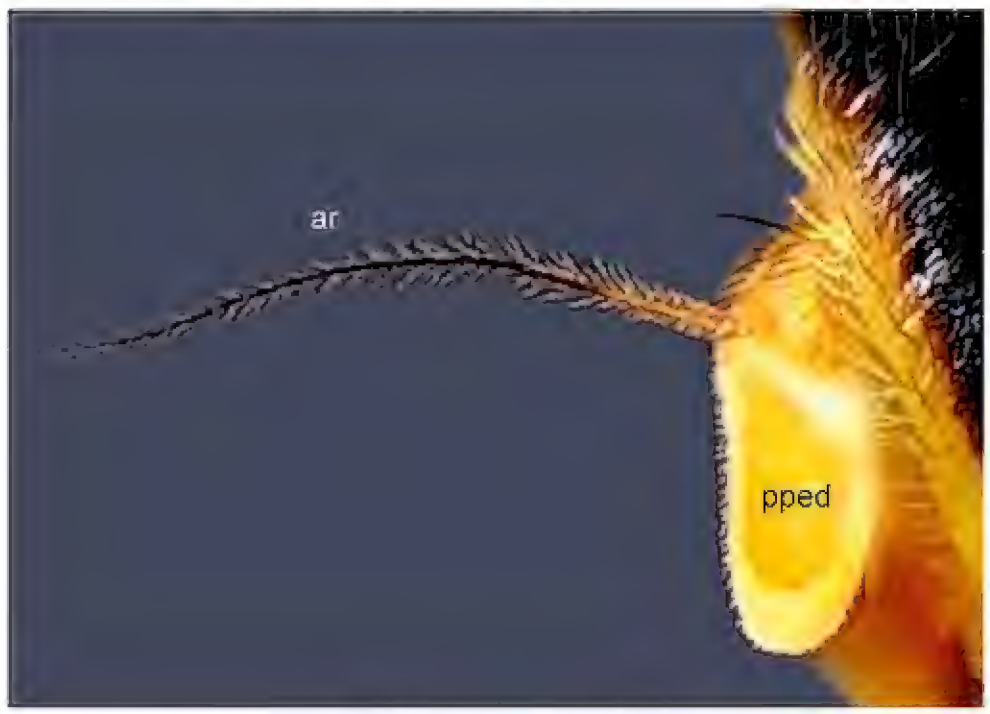
80 *Sphenoprosopa* ♂



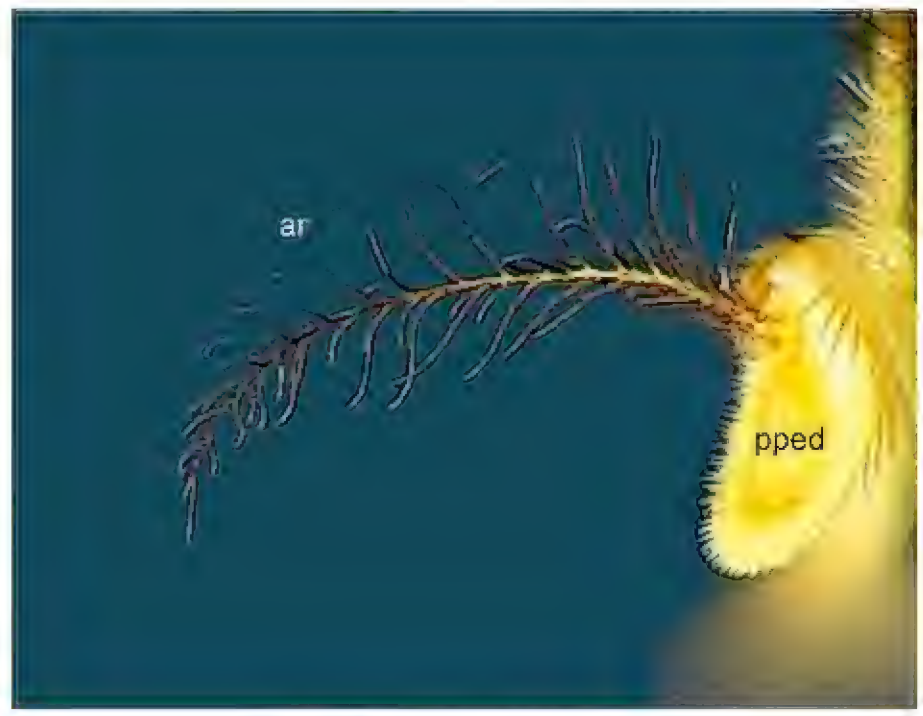
81 *Scholastes* ♂



82 *Traphera* ♂



83 *Agrochira* ♂



84 *Conopariella* ♂

Figs 70.80–84. Heads and antennae of Platystomatidae (lateral views): (80) head of *Sphenoprosopa fascipennis* Macquart ♂; (81) same, *Scholastes vicarius* Hendel ♂; (82) same, *Traphera chalybea* Wiedemann ♂; (83) antenna of *Agrochira corniculata* Whittington ♂; (84) same, *Conopariella tibialis* (Hendel) ♂.

Abbreviations: ar – arista; fc – face; pped – postpedicel; orb s – orbital seta(e).

part representatives of the subfamily require taxonomic treatment. Distinguishing features include the following: both the upper and lower calypters form a distinct lobe (or equally undeveloped in some genera); the katepisternal seta is invariably absent; tergite 5 is well-developed (in some females this may be shorter than tergite 3); with elongate terminal filaments on the sclerotised glans of the male phallus, each terminating in a gonopore; and the female aculeus is slender with a rounded apex. The following Afrotropical genera are included in the subfamily (subgenera in parenthesis): *Boisduvalia* Robineau-Desvoidy; *Bromophila*; *Clitodoca*; *Coelocephala* Karsch; *Elassogaster*; *Engistoneura* Loew; *Eosamphicnephes* Frey; *Icteracantha*; *Lambia* Hendel; *Lamprophthalma* Portschinsky; *Lophoplatystoma* Hendel; *Loxoceromyia* Hendel; *Lulodes*, *Mezona* Speiser; *Neoardelio* Hendel; *Neoepidesma* Hendel; *Oedemachilus* Bigot; *Palpomya* Robineau-Desvoidy; *Peltacanthina* Enderlein (subgenera: *P.* (*Engistoneuroides* Hendel) and *Peltacanthina sensu stricto*); *Phlebophis*; *Phytalmodes*; *Plagiostenopterina*; *Polystodes* Robineau-Desvoidy; *Pseudepicausta* Hendel (subgenera *P.* (*Parepicausta* Enderlein) and *Pseudepicausta sensu stricto*); *Rivellia*; and *Sphenoprosopa* Loew.

Scholastinae (Figs 6, 13) is a moderately large subfamily, with an estimated *ca* 144 species globally (Whittington, unpubl.). The Afrotropical fauna comprises five genera, with 30 species. Identification of the group is impeded by the lack of complete species identification keys, and for the most part, the subfamily requires taxonomic revision. McAlpine (2001) expressed doubts that the subfamily group is monophyletic, but the distinction from Platystomatinae is, nevertheless, clear and unambiguous and this is perhaps an indication that the world genera of Scholastinae require more thorough analysis. Distinguishing features include the following: the face is invariably concave below the antennal insertions (Fig. 81); the antennal arista is bare or pubescent, sometimes with long pubescence and the individual branches are straight; the katepisternal setae (Fig. 85) are invariably present (easily damaged, so it is necessary to check for alveoli; McAlpine (2001) noted this to be a poor diagnostic character at the subfamily level), or if absent (*e.g.*, *Naupoda,* Fig. 6), then the abdomen is subglobose, with abdominal tergite 3 enlarged and convex; both the upper and lower calypters form a distinct lobe; tergite 5 is shorter than tergite 3 (especially in females, in which tergite 3 is sometimes enlarged and tergite 5 absent); the male phallus has a glans without elongate terminal filaments, but if present then these filaments are short, forming a V-shape; the female tergite 6 is absent; and the female aculeus is slender, with a rounded apex. The following Afrotropical genera are included in the subfamily: *Naupoda*; *Parardelio*; *Paryphodes*; *Pseudoscholastes* and *Scholastes*.

Trapherinae (Figs 31, 56) is a small subfamily, with an estimated *ca* 35 species globally (Whittington, unpubl.). The Afrotropical fauna comprises four genera with 13 species. Steyskal (1990) reviewed the Afrotropical genera of Trapherinae, redefining this and other subfamilies and provided a diagnostic identification key to the newly described genus *Seguyopiara* Steyskal. He further split the monotypic genus *Microlule* Steyskal from *Lule*; an action later regarded by McAlpine (2001) as without foundation and this genus is consequently omitted from the below identification key, with its single species *M. flavimana* Steyskal, 1990, here ascribed to the genus *Lule*. Distinguishing features of the subfamily include the following: both the upper and lower calypters forming a distinct lobe; the katepisternal setae are invariably present; the branches of the antennal arista are long bipectinate; the face is flattened or convex and bulging outwards below the insertion of the antennae and/or extends well below the ventral-most point of the gena (Fig. 82); tergite 5 is about the same length as tergite 3; the male phallus is largely membranous and inflated, with a single sclerotised longitudinal strip, which is apically expanded and has neither a glans, nor elongate terminal filaments; female tergite 6 is well-developed and exposed; and the female aculeus is broad and acute. The following Afrotropical genera are included in the subfamily: *Lule*; *Piara* Loew; *Seguyopiara* and *Traphera*.

Identification

There are relatively few published identification keys to Afrotropical Platystomatidae, notably for the genera: *Lule* (Steyskal 1960: 315); *Neoepidesma* (Steyskal 1964), *Neoardelio* (Whittington 2000*b*) and *Seguyopiara* (Steyskal 1990). Other treatments, including those for the genera *Paryphodes* (Steyskal 1965*b*) and *Rivellia* (Frey 1932) and the subfamily Plastotephritinae (Frey 1932), are either partial and incomplete, or have been subsequently revised, as is the case for the Plastotephritinae as a whole (Whittington 2003). While numerous Afrotropical genera (17) are monotypic, or are known from only two species, lack of published generic identification keys (other than that of Hendel 1914*a*) has hindered identification, especially for the larger genera *Peltacanthina* and *Rivellia*. A manuscript generic identification key drafted by the late George C. Steyskal is available and was improved upon for this publication.

Generally, the status of Afrotropical genera appears stable, but as noted above, some characters shared between subfamilies require further examination. Despite this shortcoming, all genera can be distinguished by reference to the identification key below, with the notable exception of the genera *Boisduvalia and Polystodes*, which were not examined as part of this study and are therefore omitted. McAlpine (2001) noted that characters of the terminalia are of major importance in our understanding of subfamilies and the same also applies to generic level diagnoses. McAlpine further noted that the arrangement of abdominal spiracles may also be of relevance, but the status of these structures remains unknown for almost all Afrotropical genera. Platystomatidae are either direct-pinned or micro-pinned in the field for later double-mounting (see Chapter 2).

Key to genera of Afrotropical Platystomatidae

1. Wing with upper and lower calypter developed into distinct lobes (e.g., Fig. 91), lower calypter often longer than upper, if lower calypter reduced and narrow, then thorax with katepisternal setae (Trapherinae), or both calypters equally vestigial (*Clitodoca*, *Icteracantha*, *Phlebophis* and *Phytalmodes*); subcostal vein (*Sc*) seldom sharply angled and evanescent (e.g., Fig. 141), more often smoothly joining

costal vein (*C*) (*e.g.*, Figs 142, 143); katepisternal seta present or absent; head (viewed in profile) seldom compressed (*e.g.*, Figs 60, 67, 68, 73–75, 78–81); male terminalia with elongate terminal filaments on phallus variably present or absent 2

– Wing with lower calypter reduced to linear fringe (*e.g.*, Fig. 89), upper calypter well-developed; subcostal vein (*Sc*) ending abruptly (*e.g.*, Fig. 139), sometimes angled sharply forward at apex, evanescent toward junction with costal vein (*C*); thorax without katepisternal seta; head (viewed in profile) frequently compressed (*e.g.*, Figs 59, 63); male terminalia without elongate terminal filaments on phallus (PLASTOTEPHRITINAE) 27

2. Thorax with katepisternal setae (*e.g.*, Fig. 85) (setae easily detach, so locate alveoli), or if absent (*e.g.*, *Naupoda*; see couplet 43), then abdomen sub-globose (*e.g.*, Fig. 6), with abdominal tergite 3 enlarged, convex; male terminalia without elongate terminal filaments on phallus. 3

– Thorax without katepisternal setae; male terminalia with elongate terminal filaments on phallus (PLATYSTOMATINAE). 4

3. Head with face invariably concave below antennal insertion (*e.g.*, Figs 81), lower facial margin jutting forwards; abdominal tergite 5 shorter than tergite 3 (especially in females, where tergite 3 sometimes enlarged and tergite 5 absent); male terminalia with phallus with glans; female tergite 6 absent; aculeus slender with rounded apex (SCHOLASTINAE) 43

– Head with face flattened to convex, bulging outwards below insertion of antennae (*e.g.*, Fig. 82), lower facial margin receding and/or extending well below ventral-most point of gena; abdominal tergite 5 *ca* same length as tergite 3; male terminalia with phallus without glans; female tergite 6 well-developed, exposed; aculeus broad with acute apex (TRAPHERINAE) 47

4. Antennal postpedicel narrow and elongate, *ca* 70% antennal length from base to apex (*e.g.*, Figs 67, 73, 79, 80); slender flies, with abdomen long, narrow, compressed; head either with 1 vestigial posterior orbital seta or without posterior orbital setae 5

– Antennal postpedicel usually short, oval, usually comprising 60% or less of antennal length from base to apex (*e.g.*, Figs 61, 62, 65, 66), but if longer (*e.g.*, Fig. 77), then arista pubescent, or body more robust and bulky or small and slender (*e.g.*, Figs 38, 52), abdomen oval to elliptical; head often with 2 orbital setae present (even if 1 pair reduced usually discernible) 11

5. Wing with radial–medial (*r–m*) and discal medial (*dm–m*) crossveins separated by less than length of *r–m* (*e.g.*, Figs 105, 134); alveoli shiny and distinct from surrounding microtrichose vestiture, resulting in a reticulate pattern (*e.g.*, Figs 27, 55, 80) 6

– Wing with radial–medial (*r–m*) and discal medial (*dm–m*) crossveins separated by more than length of *r–m* (*e.g.*, Fig. 94); without reticulate pattern resulting from contrast between alveoli and surrounding vestiture (*e.g.*, Figs 21, 30, 47, 49, 67) 7

6. Antennae inserted dorsal to middle of compound eye (Fig. 27) . . . . . *Lambia* Hendel

– Antennae inserted ventral to middle of compound eye (Figs 55, 80). . . . . *Sphenoprosopa* Loew

7. Wing cell r_{4+5} not strongly narrowed toward apex; veins R_{4+5} and M_1 parallel, not bent prior to meeting costal vein (C) (*e.g.*, Fig. 128) 8

– Wing cell r_{4+5} narrowed toward apex (*e.g.*, Figs 99, 125), sometimes only slightly so, but widest part of cell situated before apex; vein R_{4+5} convergent with vein M_1 prior to meeting costal vein (*C*) 10

8. Head with frons smoothly curved in front of ocellar triangle (Fig. 79), or at most slightly carinate; with lateral postocular seta (also apparent in *Elassogaster*, *Plagiostenopterina* and *Rivellia* (Fig. 74)). . . . . *Pseudepicausta* Hendel

– Head with anterior ⅓ of frons tuberculate, bulging (*e.g.*, Fig. 67), resulting in concave depression on central frons, immediately in front of ocellar triangle; without lateral postocular setae (*e.g.*, Fig. 67) 9

9. Head without posterior orbital setae (Fig. 67); wing with crossveins *r–m* and *bm–m* markedly oblique (Fig. 106) . . . . . *Lamprophthalma* Portschinsky

– Head with posterior orbital setae; wing with crossveins *r–m* transverse and *bm–m* only weakly oblique (Fig. 108) . . . . . *Loxoceromyia* Hendel

10. Fore femur with ventral setae arising from small tubercles (Fig. 149); head with face invariably bare, without microtrichose pile; thorax brown, often with metallic green or blue iridescence (Figs 4, 5); scutellum with fine white discal setae restricted to lateral position, but absent on central disc (Fig. 87); wing cell r_{4+5} narrower at apex than midway along terminal portion of vein M_1; apex of vein M_1 curved toward apex of vein R_{4+5}, terminating anterior to wing apex (Fig. 99) . . . . . *Elassogaster* Bigot

– Fore femora without ventral spines or setae (Fig. 150); head with face sometimes microtrichose centrally beneath antennae (Fig. 73); thorax brown or grey (Figs 11, 47), if metallic iridescence present, then this weakly developed; scutellum with fine white background setae throughout (Fig. 88); wing cell r_{4+5} slightly narrower at apex than midway along terminal portion of vein M_1; apex of veins R_{4+5} and M_1 slightly convergent toward wing apex; vein M_1 terminating at or posterior to wing apex (Fig. 125) . . . . . *Plagiostenopterina* Hendel

11. Head with ocelli vestigial (Fig. 60); head setation vestigial; body and wing entirely black, with blue iridescence (wing black without hyaline patterns (Fig. 94)), head red to orange-red and rough textured (Figs 2, 16, 60); sluggish flies, not readily taking to flight . . . . . *Bromophila* Loew

– Head with ocelli normal (e.g., Fig. 68); head setation normal, orbital and vertical setae present; body and wings variously coloured, but not as described above; active flies, readily taking flight 12

12. Lower calypter noticeably enlarged, rounded, extending posteriorly, at least 2 × as large as upper calypter (Fig. 91) . . . . . *Palpomya* Robineau-Desvoidy

– Lower calypter usually smaller than upper calypter, but if larger, then < 2 × as large as upper calypter 13

13. Scutellum with marginal setae (and sometimes postalar setae), inserted on raised tubercles (Fig. 86). . . . . *Peltacanthina* Enderlein

– Scutellum with marginal setae and postalar setae not inserted on raised tubercles 14

14. All femora with distinct rows of ventral spines (Figs 147, 148); body setation prominent (Fig. 26); tarsomeres large and strongly setulose; wing with basal cells (*bm* and *cua*) prolonged (Figs 26, 104), with crossvein *bm–m* and vein *CuA* in line with apex of the subcostal vein (*Sc*) and with *r–m* and *dm–m* crossveins separated by less than length of *r–m* (Figs 26, 104); thorax orange in contrast to metallic blue abdomen (Fig. 26) . . . . . *Icteracantha* Hendel

– Mid- and hind femora without distinct rows of ventral spines; setation less obviously strong; other characters not in the above combination 15

15. Wing vein R_{2+3} strongly sinusoidal, tracing deep loop across cells r_1 and r_{2+3} (e.g., Figs 96, 123) 16

– Wing vein R_{2+3} weakly sinusoidal to straight, not tracing deep loop across cells r_1 and r_{2+3} (e.g., Fig. 124). 17

16. Ground colour metallic blue; head setae unusually short (Fig. 61); wing not broad, membrane dark brown, with 1 or 2 hyaline maculae in cell r_{2+3} adjacent to crossvein *r–m* and sometimes in cell m_4 (Fig. 96); subcostal vein (*Sc*) ending abruptly, not turning to join costal vein (*C*) (Fig. 140); crossvein *dm–m* joining vein M_1 at an acute angle (Fig. 96); male head with gena sometimes modified into elongate, spatulate protrusion (Fig. 61) . . . . . *Clitodoca* Loew

– Ground colour brown (thorax with fine silver pruinescence) (Fig. 45); head setae with inner and outer vertical setae unusually long; wing broad, membrane dark brown, with 2 hyaline maculae distal to crossvein *r–m* in cell r_{4+5} and distinct hyaline triangles along wing margin either side of apex of vein R_1 and either side of crossvein *dm–m* (Fig. 123); subcostal vein (*Sc*) angled sharply toward costal vein (*C*) at apex, but not evanescent; crossvein *dm–m* bent midway, resulting in cell *dm* being subacute at apex (Fig. 123); male head with gena unmodified . . . . . *Phlebophis* Frey

17. Head with gena unusually shaped, extending lateroventrally as cone-shaped extensions (Fig. 72); wing vein R_{4+5} and apex of vein M_1 both tracing distinctive parallel, anteriorly curving arc before terminating either side of wing tip (Fig. 124); subcostal vein (*Sc*) evanescent before junction with costal vein (*C*) (Fig. 141); membrane brown at base, with brown chevron-like cross bars at wing apex, forming inverted V-shape (Fig. 124) . . . . . *Phytalmodes* Bezzi

– Head with gena normally shaped; wing vein R_{4+5} and apex of vein M_1 more or less straight (e.g., Fig. 107); subcostal vein (*Sc*) complete (Fig. 143); membrane brown, with various hyaline patterns of maculae or fasciae 18

18. Ground colour of thorax and wing grey or grey-brown (Figs 29, 107); body densely silver-grey pruinose, except at bases of setulae, where pruinescence absent, resulting in small dark grey maculae, set in reticulated silver pattern (Fig. 29); wing membrane dark grey with discrete dense, small hyaline maculae (Fig. 107); veins R_{4+5} and M_1 diverging midway adjacent to cell r_{4+5}, then converging again prior to wing apex (Fig. 107). . . . . *Lophoplatystoma* Hendel

– Ground colour of thorax and wing not predominantly grey; body usually without reticulated silver pattern, but if reticulate, then wing banded, without hyaline maculae; if wing with basal maculae, then thorax either entirely microtrichose or entirely bare, but not reticulate (e.g., Figs 97, 110, 118); vein R_{4+5}

and M_1 not diverging midway and then converging, if diverging, then gradually so toward wing apex (e.g., Figs 97, 110, 118) 19

19. Wing with *r–m* and *dm–m* crossveins closely approximated, separated by less than length of *r–m* (e.g., Fig. 118) 20

– Wing with *r–m* and *dm–m* crossveins separated by more than length of *r–m* 21

20. Wing vein M_1 beyond cell *dm* sinusoidal, consequently not parallel to apical portion of vein R_{4+5}; body dark brown . . . . . *Eosamphicnephes* Frey

– Wing vein M_1 beyond cell *dm* weakly curved, parallel to apical portion of vein R_{4+5} (Fig. 118); body with violet reflections evident on otherwise brown thorax (Fig. 40) . . . . . *Oedemachilus* Bigot

21. Head with posterior orbital setae strongly reduced, vestigial and difficult to discern (e.g., Fig. 62) . . . 22

– Head with both orbital setae normal, sometimes one reduced in size (e.g., *Neoepidesma*, Fig. 77), but invariably evident 23

22. Wing (Fig. 97), with cell *dm* wider at apex than at base; vein M_1 bowed into cell *dm* proximal to *r–m*; basal radial cell (*br*) long, sub-rectangular; membrane fasciate or maculate, but without noticeable blister-like hyaline maculae; head with vertex slightly sunken in frontal view (Fig. 62) . . . . . *Coelocephala* Karsch

– Wing (Fig. 110), with cell *dm* large, rectangular, dominating central wing membrane; basal radial cell (*br*) narrow, distorted; membrane with blister-like hyaline maculae, most evident in basal cells; head with vertex not noticeably sunken . . . . . *Lulodes* Speiser

23. Large species (wing span: > 18 mm); head with well-developed flat, sharp-edged facial carina, separating antennal insertions (e.g., Figs 65, 66, arrowed) 24

– Small species (wing span: < 15 mm); head with undeveloped facial carina 25

24. Head with antennal insertions approximately separated by width of scape (Fig. 65, arrowed); posterior orbital seta fine, indistinct; 2 pairs of vertical setae evident (Fig. 65) . . . . . *Engistoneura* Loew

– Head with antennal insertions separated by less than width of scape (Fig. 66, arrowed); posterior orbital seta distinct; 1 pair of vertical setae evident (Fig. 66) . . . . . *Mezona* Speiser

25. Fore femur without ventral setae longer than general vestiture; wing vein M_1 straight (not, or very slightly bowed into cell *dm* proximal to *r–m* crossvein) (Fig. 115) . . . . . *Neoardelio* Hendel

– Fore femur with 2 or more dorsal or posterodorsal and posteroventral setae, toward apex in addition to shorter vestiture (e.g., Fig. 154); wing vein M_1 bowed into cell *dm* proximal to *r–m* crossvein (e.g., Fig. 131, arrowed) 26

26. Head with 1 pair of orbital setae positioned forward of anterior ocellus (Fig. 77); with 1 pair of scutellar marginal setae, noticeably long, reaching beyond apex of abdominal tergite 1 + 2 . . . . . *Neoepidesma* Hendel

– Head with 2 distinct pairs of orbital setae, or posterior orbital seta diminutive, reduced in size; with 2 pairs of scutellar marginal setae, medial pair occasionally reaching apex of abdominal tergite 1 + 2, but if so, then invariably with additional lateral pair present . . . . . *Rivellia* Robineau-Desvoidy

27. Antennal arista pubescent (e.g., Fig. 83); head with outer and inner vertical setae 28

– Antennal arista plumose (e.g., Fig. 84); head with only outer vertical setae strongly developed, inner vertical setae reduced, setula-like, often indistinguishable from postocellar setae 34

28. Wing membrane brown, with hyaline maculae and fasciae (e.g., Figs 25, 92, 103, 111, 113); fore femora with distinct row of spines (e.g., Figs 145, 146) on ventral surface (may be present only as small tubercles in females, e.g., *Mesanopin tridens* Whittington, 2003) 29

– Wing membrane with radiate brown pattern (e.g., Figs 17, 23, 95, 101, 135), sometimes combined with maculae; fore femora sometimes distinctly setose, at most with single ventral spine 32

29. Scutellum with 2 pairs of marginal setae. . . . . *Furcamyia* Whittington

– Scutellum with 3 pairs of marginal setae. 30

30. Head with inner vertical setae clearly shorter and weaker than outer vertical setae; thorax with notum strongly microtrichose; hind trochanter with setulose ventral lobe; hind tibia bent inwards at apex . . . . . *Micronesomyia* Whittington

– Head with inner vertical setae equal (or similar in length) to outer vertical setae (not distinctly weaker); thorax with notum without distinct patterns of microtrichia; hind tibia normal 31

31. Wing membrane without hyaline maculae in cell r_{2+3} (Fig. 92); male terminalia with lateral surstyli elongate, equal to (or longer than) length of epandrium; female terminalia with aculeus tip sharply pointed (Fig. 160) . . . . . .*Agrochira* Enderlein

– Wing membrane frequently with maculae in cell r_{2+3} (Fig. 111); male terminalia with lateral surstyli reduced, much shorter than length of epandrium; female terminalia with aculeus tip bluntly rounded (Fig. 161) . . . . . .*Mesanopin* Enderlein

32. Thorax without postpronotal setae; head, scutellum and abdomen with conspicuous white setae, interspersed among black setae (Figs 23, 69); head with orbital plate beset with dense tufts of setae (Fig. 69). . . . . *Eudasys* Whittington

– Thorax with postpronotal setae; head, scutellum and abdomen with setae inconspicuous and sparse; head with orbital plate never beset with dense tufts of setae 33

33. Head with orbital setae compressed, distinctly broader in lateral view than in frontal view; male fore femur strongly setose ventrally, setae inserted normally; male hind trochanter with long, curved, posteriorly directed spur on ventral surface and compact knob on inner dorsal surface; male hind tibiae simple . . . . . *Cladoderris* Bezzi

– Head with orbital setae round in cross-section, not distinctly compressed; male fore femur with at most 1 spine present, otherwise usually strongly setose ventrally, inserted on small tubercles (inserted normally in females); male hind trochanter rounded on inner ventral margin; male hind tibiae swollen at apex, slightly concave, concavity bounded by dense fringe of black setae . . . . . *Stellapteryx* Whittington

34. Scutellum with 3 pairs of marginal setae (unusually 4 pairs in *Atopocnema*) 35

– Scutellum with 2 pairs of marginal setae. 40

35. Head with lower facial margin strongly protruding forward to beyond apex of antenna . . . . . *Prosopoconus* Enderlein

– Head with lower facial margin not protruding farther than base of antenna 36

36. Abdomen strongly sclerotised and sculptured, hemispherical in shape (tergites arching around laterally and distally to form concave shell) (Figs 7, 39) . . . . . .*Oeciotypa* Hendel

– Abdomen not heavily sclerotised, not sculptured, ovoid to elongate in shape, slightly dorsoventrally compressed or cylindrical (not forming concave shell) 37

37. Thorax with prescutellar acrostichal setae present; head with face and frons narrow (*ca* as wide as length of antennae); frons between ptilinal fissure and medial ocellus $< 2 \times$ as broad as long 38

– Thorax without prescutellar acrostichal setae; head with face and frons broad (wider than length of antennae); frons at least $2 \times$ as broad as long 39

38. Wing (Fig. 93) invariably with setae on radial sector (*Rs*) and *Cu*; antennal arista long plumose (dorsal and ventral branches combined exceeding width of postpedicel); hind trochanter with outer margin sometimes extended into lobe; male hind tibia swollen at apex, to almost $2 \times$ width of base of tibia, terminating in acute angle on outer margin, with this surface glabrous, slightly concave, bounded by dense fringe of black setae . . . . . *Atopocnema* Enderlein

– Wing (Fig. 137) invariably without setae on vein *Cu*, usually absent on radial sector (*Rs*); antennal arista short plumose (dorsal and ventral branches combined less than, or equal to, width of postpedicel); hind trochanter with inner surface distally extended as lobe; male hind tibia either unmodified, or modification only slight, not readily discernible, without border fringe. . . . . .*Venacalva* Whittington

39. Head of male rounded to oval in frontal view, with gena unmodified; gena deep (> 0.2 of height of head in frontal view); face flat, lower facial margin in approximately same plain as face (Fig. 48), an even curve in frontal view; male hind tibia straight, apex not elaborately modified . . . . . *Plastotephritis* Enderlein

– Head of male triangular in frontal view, with gena expanded laterally; gena shallow (< 0.15 of height of head in frontal view); face tuberculate or concave, lower facial margin protruding forward beyond line level with apex of antennal pedicel; male hind tibia with apex elaborately modified . . . . . *Xyrogena* Whittington

40. Thorax with postpronotal setae; notum without prescutellar acrostichal setae; wing (Fig. 130) with setae sometimes present ventrally on vein R_1 basal to pterostigma and/or on base of R_{4+5}, in addition to setae dorsally along length of veins R_1 and R_{4+5}, but never along vein R_{2+3} or on vein M_1; wing longitudinally fasciate (Fig. 130); head with posterior orbital seta reduced, and flattened or compressed; large species (for Plastotephritinae) (wing length: > 6.9 mm) . . . . . *Pterogenomyia* Hendel

– Thorax without postpronotal setae; notum with prescutellar acrostichal setae; wing with setae ventrally on veins R_{2+3} and/or on M_1, in addition to setae dorsally along length of veins R_1 and R_{4+5};

wing membrane (e.g., Figs 98, 102) generally dark brown, with hyaline maculae and incisions (not longitudinally fasciate); head with posterior orbital seta at most slightly shorter than anterior orbital seta, round in cross-section; small species (wing length: < 6.5 mm) 41

41. Medial wing vein (M_4) without dorsal row of setae (Fig. 98) . . . . *Conopariella* Enderlein [in part; most]

– Medial wing vein (M_4) with dorsal row of setae (e.g., Fig. 102) 42

42. Male terminalia with medial surstylus modified at apex, hooked and sickle-shaped, or with extended apical lobe; stem of medial surstylus lacking outward projecting hook; larger species (male body length: 3.5–3.9 mm; wing length: 4.0–4.9 mm; female body length: 3.2–5.5 mm; wing length: 3.9–5.5 mm) (*C. exigua* Whittington, 2003 & *C. paucifenestrata* (Steyskal, 1963). . . . *Conopariella* Enderlein [in part]

– Male terminalia with medial surstylus bilobed at apex, with outwardly directed hook midway along stem, which articulates with notch in lateral surstylus; smaller species (male body length: 2.7–3.3 mm; wing length: 2.7–3.8 mm; female body length: 2.7–3.4 mm; wing length: 2.9–3.8 mm) . . . . . *Federleyella* Frey

43. Wing with basal medial (*bm*) and anterior cubital (*cua*) cells considerably widened, squashing basal radial cell (*br*) and radial sector (*Rs*) toward costal vein (*C*), thus *r–m* crossvein noticeably shorter than *bm–m* crossvein (Fig. 114); head with orbital setae vestigial or small, if present then paired and body distinctly subglobose (Fig. 6), with enlarged abdominal tergite 3; compact body form: head closely attaching to thorax, vertex fairly acute; scutum and scutellum closely attached (both densely punctate, often metallic) and abdomen closely attaching to thorax; wings usually folded around apex of abdomen at rest (Figs 35, 36); abdominal tergite 1+2 sometimes greatly reduced, partly concealed beneath scutellum; abdominal tergite 3 occupying approximately ½ of abdomen length; tergites 4 and 5 sometimes membranous in females; thorax without katepisternal seta (unusual in subfamily) . . . . . .*Naupoda* Osten Sacken

– Wing with width of basal medial cell (*bm*) at widest point subequal to width of basal radial cell (*br*) at apex (e.g., Figs 121, 129, 132); head with posterior orbital setae well-developed; head not unusually closely attaching to thorax (e.g., Fig. 13); abdominal tergites not differing greatly in size; tergites 4 and 5 sclerotised in females; thorax with katepisternal seta at posterodorsal margin 44

44. Thorax noticeably broad, as broad as or broader than entire length of thorax, including scutellum; wing vein R_{4+5} sinusoidal beyond *r–m* crossvein *and* vein M_1 strongly curved proximal to *r–m* (Fig. 129); antennal arista spatulate at apex (Fig. 76). . . . . *Pseudoscholastes* Frey

– Thorax not noticeably broad, either approximately equal to thorax and scutellum, or longer than broad; wing vein R_{4+5} straight or gently curved beyond crossvein *r–m* and vein M_1 usually straight or gently curved proximal to *r–m* (e.g., Figs 120, 132) or curved in *Paryphodes* (Fig. 121), but then R_{4+5} is straight; antennal arista not spatulate at apex 45

45. Antennal arista with long, bipectinate branches (Fig. 81); head with 1 orbital seta (Fig. 81); distinctively marked species; frons with raised transverse ridge on lower ⅓ above ptilinal fissure (Fig. 68); wing vein R_{2+3} sinusoidal (Fig. 132) . . . . . *Scholastes* Loew

– Antennal arista with short, non-seriate branches; head with 2 pairs of orbital setae; not distinctively marked species; frons without raised transverse ridge (e.g., Figs 70, 71); wing vein R_{2+3} straight to slightly wavy (e.g., Figs 120, 121). 46

46. Head with frons (in frontal view), strongly narrowing toward vertex (Fig. 70) . . . . . *Parardelio* Hendel

– Head with frons (in frontal view), weakly narrowing, parallel-sided (Fig. 71), or widening toward vertex. . . . . *Paryphodes* Speiser

47. Wing with pterostigma virtually absent; subcostal cell (*sc*) narrow, with subcostal vein (*Sc*) and vein R_1 meeting costal vein (*C*) very close together. . . . . *Piara* Loew

– Wing with pterostigma normally developed; subcostal cell (*sc*) wider, with subcostal vein (*Sc*) and vein R_1 meeting costal vein (*C*) farther apart (e.g., Figs 109, 133, 136) 48

48. Scutellum with 2 pairs of marginal setae; wing with apex of basal medial cell (*bm*) not noticeably widened and crossvein *dm–m* perpendicular to vein M_1 (Fig. 133). . . . . *Seguyopiara* Steyskal

– Scutellum with 3 pairs of marginal setae; wing with apex of basal medial cell (*bm*) noticeably widened (e.g., Fig. 109) or crossvein *dm–m* acutely angled (e.g., Fig. 136) 49

49. Wing (Fig. 136) with basal medial crossvein (*bm–m*) ½ as long as vein *Cu* or shorter; cell *br* not noticeably altered by shape of cells *bm* and *dm*, which are not considerably widened, thus not compacting cell *br* and radial sector (*Rs*) toward costal vein (*C*), consequently *r–m* ½ as long as *bm–m* . . . . . *Traphera* Loew

– Wing (Fig. 109) with basal medial crossvein (*bm–m*) > ½ as long as vein *Cu*; cell *br* noticeably deformed as a consequence that cell *bm* and base of cell *dm* are considerably widened (except in *L. brincki* Steyskal, 1960), thus compacting cell *br* and radial sector (*Rs*) toward costal vein (*C*), consequently *r–m* less than ½ as long as *bm–m* . . . . . *Lule* Speiser

Synopsis of the fauna

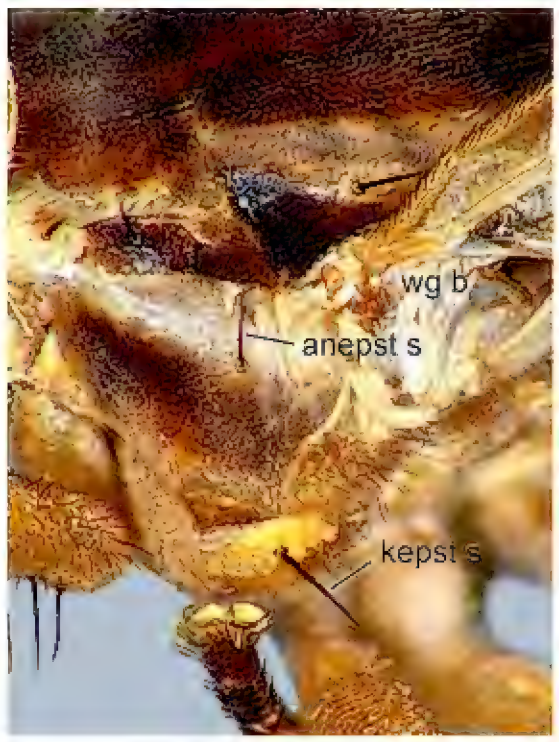
The family Platystomatidae comprises 128 described genera and 1,164 species globally (Pape *et al.* 2011), with assessment of more accurate figures inhibited by the general need for improved taxonomic revision. McAlpine (2001), for example, estimated that there are *ca* 220 species awaiting description from the Australasian Region, suggesting that the total count for that region may be 900 or more species. In the Afrotropics 51 genera are known and there are over 300 described species (updated from Whittington 2009: 303). Kirk-Spriggs & Stuckenberg (2009: 186) predicted that there are likely to be 70+ undescribed species in the region, representing 20% of the entire fauna. In contrast, the Palaearctic Region has *ca* 52 species (Soós 1984: 38), the Oriental Region 260 species (Steyskal 1977: 135), the Nearctic Region 41 species (Steyskal 1965*a*: 655) and the Neotropical Region rather fewer, with 26 species (Steyskal 1968: 1; Whittington 2010: 903).

Agrochira **Enderlein** (Plastotephritinae)**.** An endemic genus of five described species (Fig. 14), distributed in Central and West Africa, with occasional specimen records from East Africa. No undescribed species are known. *Agrochira* are small flies (body length: < 10 mm), with yellow and brown bodies and distinctively dark brown wings (Figs 14, 92), marked along the margins by hyaline maculae. They are sexually dimorphic, with males having the parafacial areas expanded, causing the development of eye stalks (Fig. 59). The male fore femora also bear stout spines ventrally (Fig. 145). In the female, the aculeus is sheath-like and hard-tipped (Fig. 160), suggesting that oviposition may take place in plant axils. *Agrochira* shares a close affinity with *Mesanopin*, another endemic genus in the region. The genus predominantly occurs in riparian vegetation in climax rainforest and tropical forests. The biology and immature stages are otherwise unknown. An identification key to the five species was provided by Whittington (2003).

Atopocnema **Enderlein** (Plastotephritinae)**.** An endemic genus of four described species (Fig. 15), distributed across Central and West Africa and in Angola and Uganda. No undescribed species are known. *Atopocnema* are small (body length: < 5 mm), pale yellow and brown flies, with dark brown wings, sometimes marked with hyaline maculae, especially along the wing margin (Figs 15, 93). The male hind tibia is distally expanded, presumably to facilitate pheromone transfer (White 1999: 508). The female aculeus is wide and flattened (softer than in *Agrochira* and *Conopariella*), with ovoid, moderately long-setulose cerci, suggesting that oviposition may take place in moderately wide opened plant axils or similar narrow and wide crevices in the substrate. *Atopocnema* shares a close affinity with *Venacalva*, another endemic genus in the region. The genus occurs predominantly in a mixture of forest and woodland vegetation types. The biology and immature stages are otherwise unknown. An identification key to the four species was provided by Whittington (2003).

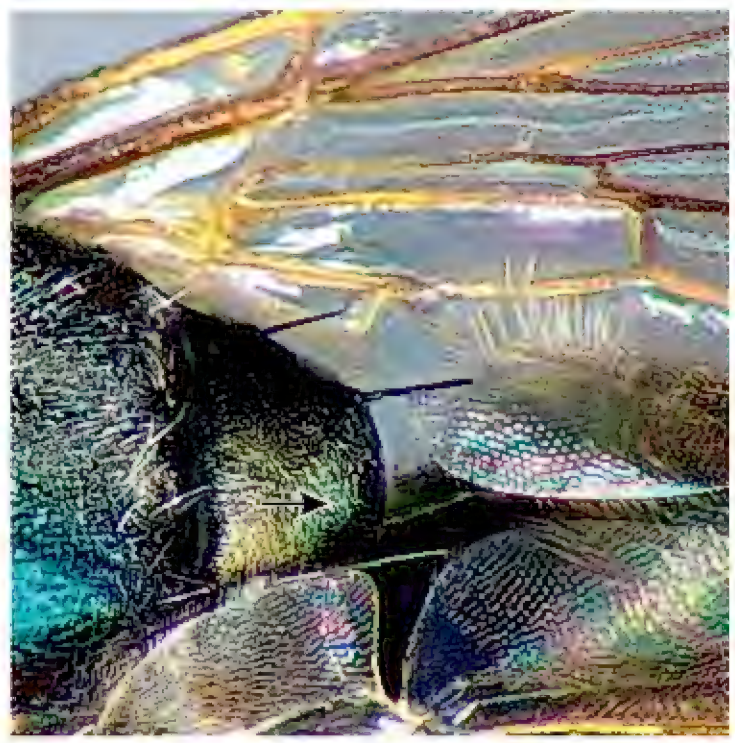
[***Boisduvalia*** **Robineau-Desvoidy** (*incertae sedis*)**.** A genus of five nominal species occurring in the Oriental and Afrotropical Regions and two *patria ignota* (Evenhuis *et al.* 2010). The type species, by the subsequent designation of Duponchel *in* Orbigny (1842: 637), is *Boisduvalia rutilans* Robineau-Desvoidy, 1830 from "Indes orientales" (possibly Indochina or Indonesia), a species with a yellowish frons, face and tarsi ("pattes"), black, violet lustrous body, *ca* 10 mm in length and the black wing with two anterior and four posterior hyaline maculae. None of the known Oriental Platystomatidae or other Tephritoidea species fit this description. Previously, Hendel (1914*a*: 169) noted that Loew (1873) tentatively synonymised this name with *Rivellia*. The actual statement by Loew (1873: 18) was "Whether the genus *Boisduvalia* really differs from the preceding [*i.e.*, *Rivellia*] only by the length of the third antennal joint [= postpedicel] seems very doubtful; should this be the case, the separation of these two genera would not be justified." Furthermore, the original description is insufficient to distinguish one from the other, except that the wing pattern was described by Robineau-Desvoidy (1830) as black and maculate, which is inconsistent with the wing patterns of any known species in *Rivellia*. Hendel (1914*a*: 169) concluded that the wing pattern of the type species, *B. rutilans*, was more reminiscent of those of the small Indian and African Tephritidae of the genera *Pseudospheniscus* Hendel and *Speniscomyia* Bezzi (currently assigned to *Sphaeniscus* Becker). The Oriental species of *Sphaeniscus*, which have a shiny black body (without a clearly violet sheen), a wing pattern as described by Robineau-Desvoidy and superficially resemble *Rivellia*, are much smaller (body length: 3.0–4.5 mm) than the *B. rutilans* type and normally have the frons, face and tarsi brown. The only other black-violet-bodied flies with dark, hyaline-maculate wings and a yellow frons are numerous species of the genus *Loxonevra* Macquart, but these all have wing patterns differing from that described by Robineau-Desvoidy by the number and position of hyaline areas. The family placement for the genus in Platystomatidae by Evenhuis *et al.* (2010) is not supported here. Specimens were not studied in preparation of this chapter and the genus is consequently omitted from the above identification key. Biology and immature stages remain unknown and no identification key to species is currently available.]

Bromophila **Loew** (Platystomatinae)**.** An endemic monotypic genus, with the single described species, *B. caffra* (Macquart, 1845) (Figs 2, 16), recorded from East and Southern Africa. This large, distinctive species has a bright red head and black body (Figs 2, 16), lacks ocelli (Fig. 60), has a slightly iridescent wing membrane (Fig. 94) and the body size ranges from 10–25 mm. The species appears to prefer *Terminalia*-veld (Combretaceae), but not to the exclusion of other vegetation types. Speiser (1910) recorded *B. caffra* from elevations of 1,300–1,900 m on Mt Kilimanjaro, Tanzania. *Bromophila* are sluggish flies, not easily taking to flight and are readily taken as food by birds (B.S. Stuckenberg, pers. comm. 1992). Adults have been observed to swarm on dung of Vervet monkey, *Chlorocebus pygerythrus* F. Cuvier (Cercopithecidae) in South Africa and to rest in large numbers on the underside of leaves in Namibia (A.H. Kirk-Spriggs, pers.



85 *Scholastes* ♂

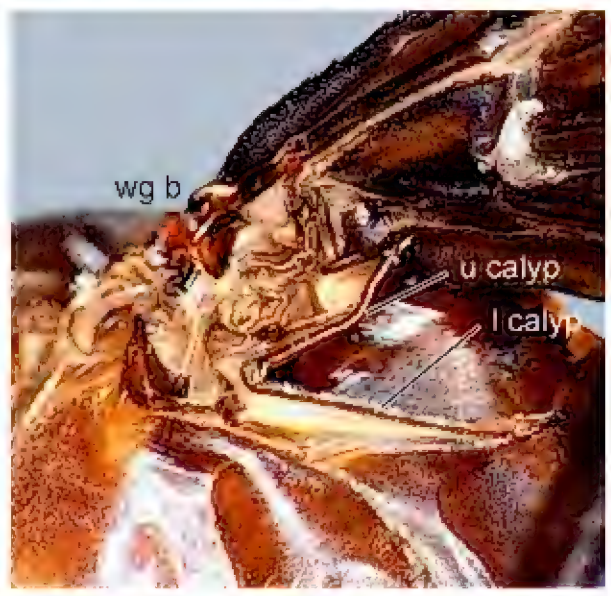
86 *Peltacanthina* ♀



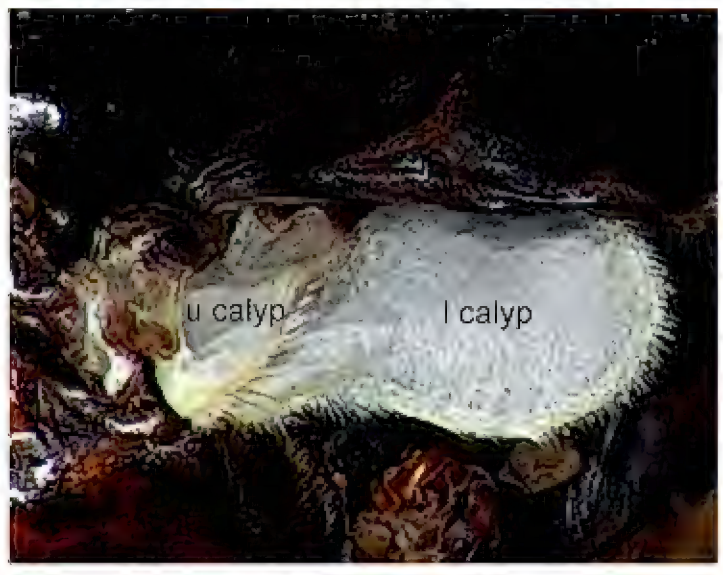
87 *Elassogaster* ♂

88 *Plagiostenopterina* ♂

89 *Agrochira* ♂



90 *Clitodoca* ♂



91 *Palpomya* ♀

Figs 70.85–91. Thoraces and calypters of Platystomatidae: (85) thoracic pleurites of *Scholastes vicarius* Hendel, oblique lateral view ♂; (86) scutellum of *Peltacanthina* sp., dorsal view ♀; (87) same, *Elassogaster* sp., oblique dorsal view ♂ (arrow indicates marginal setulae); (88) same, *Plagiostenopterina* sp. ♂ (arrows indicate marginal and discal setulae); (89) calypter of *Agrochira corniculata* Whittington, lateral view ♂; (90) same, *Clitodoca fenestralis* (Macquart) ♂; (91) same, *Palpomya asphaltina* (Wiedemann) ♀.

Abbreviations: anepst s – anepisternal seta; kepst s – katepisternal seta; l calyp – lower calypter; l calyp fr – lower calypter fringe; sctl tub – scutellar tubercles; u calyp – upper calypter; wg b – wing base.

obs.). Superficially the species could be confused with similarly coloured species assigned to the genera *Engistoneura* and *Peltacanthina*, but the absence of ocelli and setae on the head, in combination with the nearly entirely black wings serve to distinguish it. No undescribed species are currently known. Biology and immature stages otherwise remain unknown.

***Cladoderris* Bezzi** (Plastotephritinae)**.** An endemic genus of four described species (Fig. 17), predominantly distributed across Central, East and West Africa and as far south as Mozambique. No undescribed species are currently known. *Cladoderris* are small flies (body length: < 5 mm), pale creamy white coloured, with brown markings (Fig. 17); the head setae are laterally compressed and the wing has a distinctive radiating pattern of brown on a hyaline membrane (Fig. 95). Sexual dimorphism is evident in the head, in which the male gena is laterally expanded (as in Fig. 64). The female aculeus varies from oval in cross-section to flattened (in *C. ornata* Whittington, 2003), with discrete, ovoid, moderately long-setulose cerci, suggesting a variety of oviposition substrates are utilised. There are no known affinities with other genera, but *Cladoderris* could be grouped with Afrotropical *Eudasys* and *Stellapteryx* and Oriental *Agadasys* Whittington (Whittington 2000*a*). The genus occurs in dense gallery forest, climax rainforest, tropical forest and swamp forest types. Biology and immature stages otherwise remain unknown. An identification key to the four species was provided by Whittington (2003).

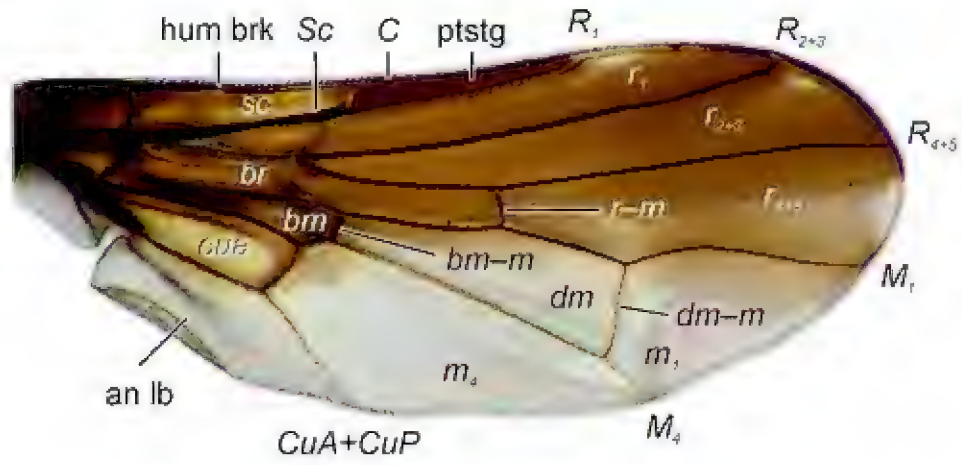
***Clitodoca* Loew** (Platystomatinae)**.** An endemic monotypic genus, with the single described species, *C. fenestralis* (Macquart, 1843), distributed in Central and West Africa, with occasional specimens noted from Angola and Uganda. No undescribed species are currently known. A large-sized (body length: 15–25 mm), distinctive blue metallic species, generally without long setae (Fig. 18); the male head is often elaborated by distinctive spatulate extensions to the gena (Fig. 61). The wing is narrow, with a black iridescent membrane (Fig. 140) and a single, or sometimes double, clear macula(e) (Fig. 96). The habitat preference appears to be climax rainforest. Biology and immature stages are otherwise unknown.

***Coelocephala* Karsch** (Platystomatinae)**.** An endemic genus of five described species (Fig. 19), distributed from Guinea to Nigeria in West Africa, across to Malawi, Rwanda, Tanzania and Uganda in Central and East Africa. No undescribed species are currently known. The genus is distinguished as follows: the frons is concave, with the vertex noticeably sunken between the orbits, such that the upper margin of the compound eyes are raised above the level of the base of the ocellar triangle (Fig. 62); the lateral postocular seta is absent; and wing crossveins *r–m* and *dm–m* are separated by more than the length of *r–m* (Fig. 97). Adults of *C. arcuata* (as *C. stigma*) have been taken in chimneys of the mounds of the termite *Macrotermes natalensis* (Haviland) (Termitidae) in Liberia, suggesting a biological association with Isoptera (Steyskal 1965*b*). Biology and immature stages otherwise remain unknown. No identification key to species is currently available.

***Conopariella* Enderlein** (Plastotephritinae)**.** An endemic genus of 12 described species (Figs 3, 20), distributed across Central, Southern and West Africa, as far south as Malawi, Mozambique and Zimbabwe, but apparently not east of the great lakes of the Albertine Rift. No undescribed species are currently known. *Conopariella* are small- to medium-sized, body length < 7 mm (3.2–5.3 mm), mostly dull yellow and brown species, with dark brown wings, sometimes marked with hyaline maculae, especially as a triangular wedge on the hind margin of the wing (Figs 3, 20). They are sexually dimorphic, with the male gena laterally expanded, giving the head a triangular appearance in frontal view (Fig. 64). The female aculeus is usually flattened, with flat, apically acute cerci, bearing moderately long lateral setulae, suggesting that eggs are inserted between tightly appressed plant axils. *Conopariella* shares a close affinity with *Federleyella*, another endemic genus, from which it is mainly distinguished by characters of the male terminalia. Both genera have the antennal arista noticeably plumose (as does *Xyrogena*) and setae on the base of vein M_4, together with veins of the radial sector (Fig. 98). The genus occurs in a wide variety of forest habitats, from coastal tropical rainforest to Afromontane forest. The genus also occurs in agricultural land. Frey (1932), for example, recorded *C. conspicua* Frey, 1932 on Maize at an elevation of 1,000 m. Biology and immature stages otherwise remain unknown. An identification key to the 12 species was provided by Whittington (2003).

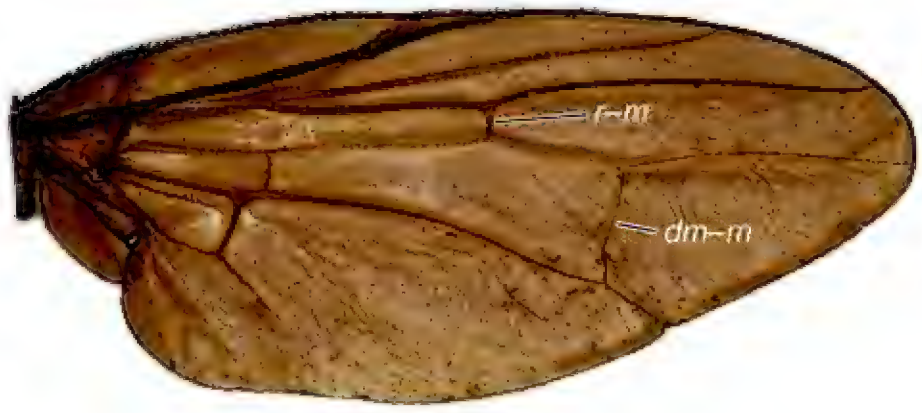
***Elassogaster* Bigot** (Platystomatinae)**.** A genus of 25 described species (Figs 4, 5, 21), occurring in the Afrotropical, Australasian, Oriental and Palaearctic Regions. Seven described species are currently known from the Afrotropics, with four undescribed species known from Angola, Democratic Republic of Congo, Kenya and Madagascar, respectively. *Elassogaster* are distinctly long, narrow flies (Figs 4, 5, 21) and can be distinguished by: wing cell r_{4+5}, which is narrowed toward the apex (Fig. 99); the orbital setae are vestigial, while a lateral postocular seta is present and distinctive (as in e.g., Fig. 74); the fore femur has ventral setae arising from small tubercles (Fig. 149); the face is invariably bare; the thorax is brown (often with a metallic green or blue iridescence); and cell *br* is clear in most species (e.g., Fig. 99). *Elassogaster* species superficially resemble, and may be confused with, species of *Plagiostenopterina and Pseudepicausta*. While many characters are shared between the three genera, such as general body form, head shape and setation, and the length of antennal postpedicel, *Elassogaster* is distinct in having a ventral series of setae on the fore femur (Fig. 149), lateral postocular seta present and setulae on the scutellum restricted to the lateral margin (Fig. 87). Biology and immature stages remain unknown. McAlpine (2001) noted that a complete taxonomic revision of the genus is needed across the full distribution range and no recent identification keys to species are available.

***Engistoneura* Loew** (Platystomatinae)**.** An endemic genus of eight described species (Fig. 22) confined to West Africa. No undescribed species are currently known. *Engistoneura* have elongate wings that are densely patterned with brown and hyaline markings (Figs 22, 100). They superficially resemble *Mezona* and some *Peltacanthina*, but can be distinguished from *Mezona* by the antennal insertions, which are separated by the width of the antennal scape (or more) and by the presence of two pairs of vertical setae (Fig. 65); and from *Peltacanthina* on the basis of the scutellum, which lacks tubercles at the base of the scutellar marginal setae. Nothing is known regarding the biology and immature stages, but the preferred habitat appears to be predominantly rainforest. No recent identification keys to species are available.

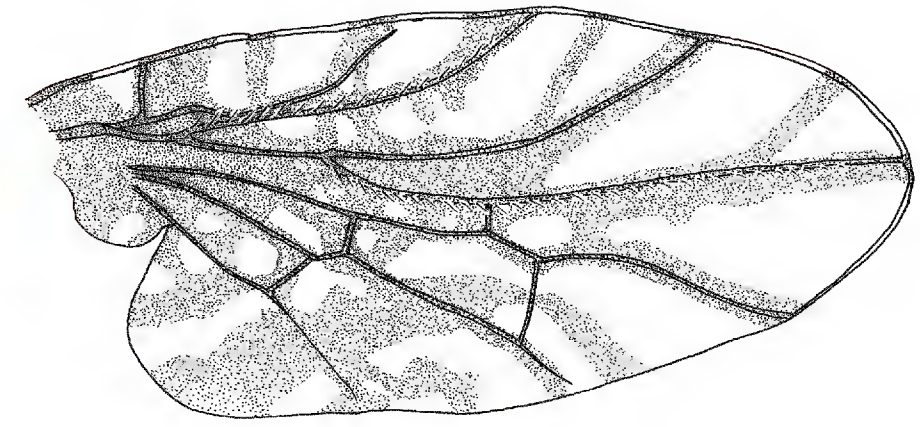


92 *Agrochira* ♂

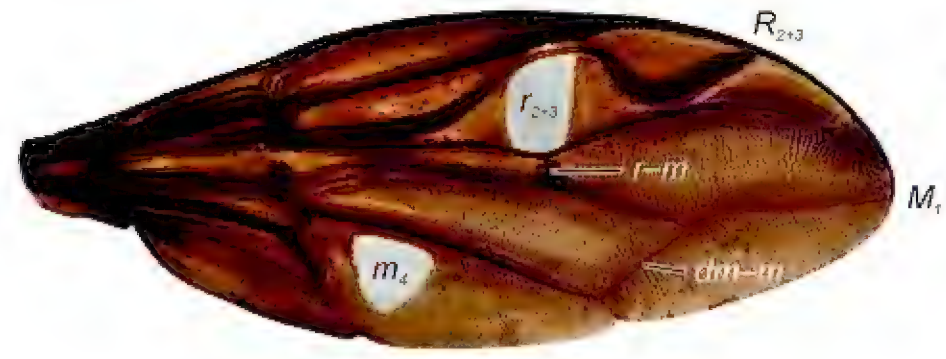
93 *Atopocnema* ♀



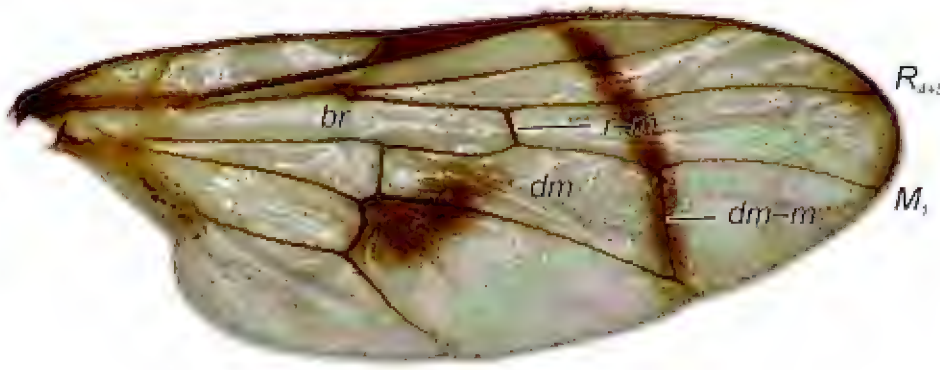
94 *Bromophila* ♂



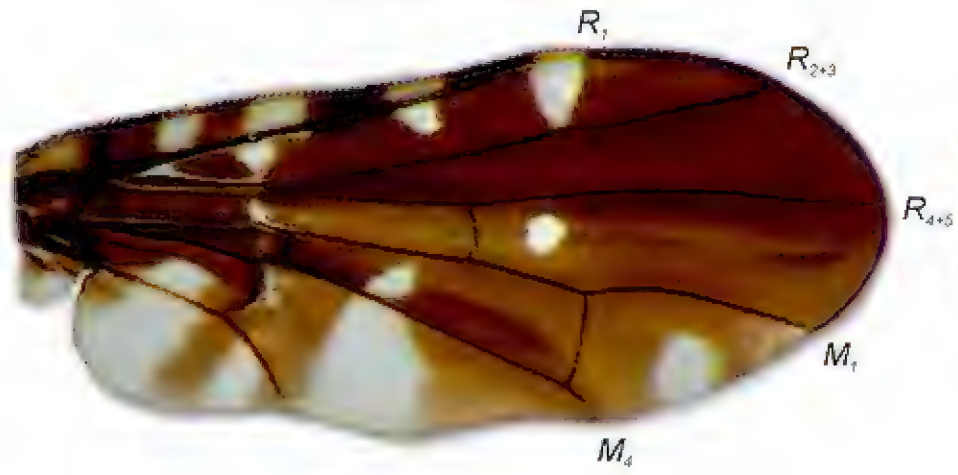
95 *Cladoderris* ♂



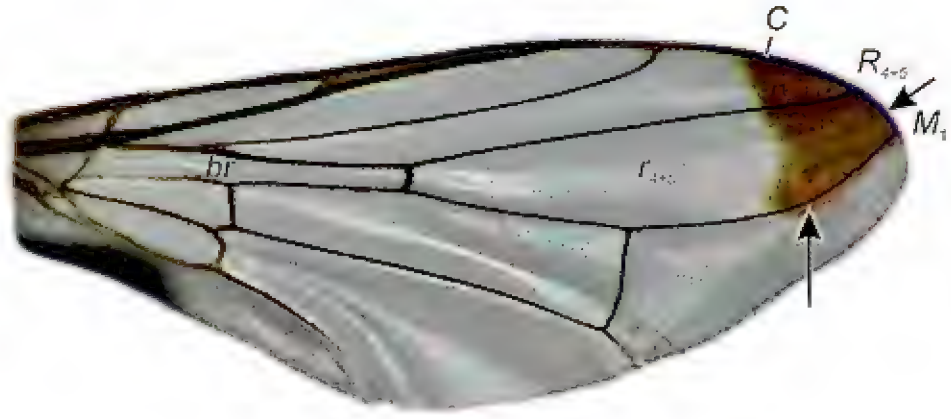
96 *Clitodoca* ♂



97 *Coelocephala* ♂



98 *Conopariella* ♀



99 *Elassogaster* ♂

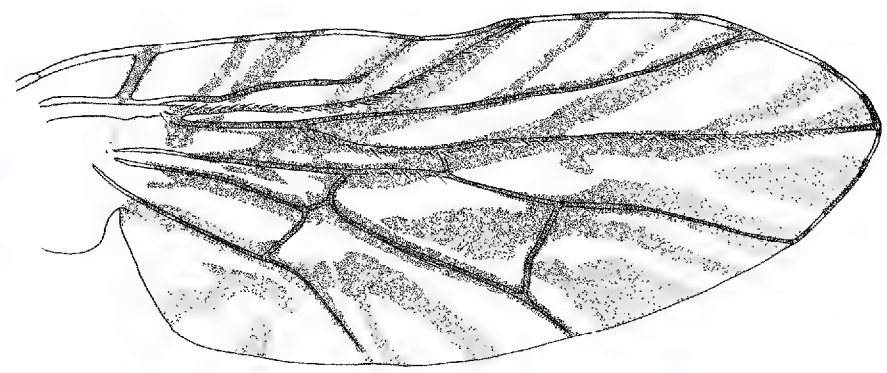
Figs 70.92–99. Wings of Platystomatidae (dorsal views): (92) *Agrochira corniculata* Whittington ♂; (93) *Atopocnema manicatifrons* Enderlein ♀; (94) *Bromophila caffra* (Macquart) ♂; (95) *Cladoderris* sp. ♂; (96) *Clitodoca fenestralis* (Macquart) ♂; (97) *Coelocephala arcuata* Bezzi ♂; (98) *Conopariella tibialis* (Hendel) ♀; (99) *Elassogaster* sp. ♂ (arrows indicate broadest (left) and narrowest (right) points of cell r_{4+5}). Fig. 95 (Whittington 2003, figs 15 and 134).

Abbreviations: an lb – anal lobe; *bm* – basal medial cell; *bm–m* – basal medial crossvein; *br* – basal radial cell; *C* – costal vein; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *dm* – discal medial cell; *dm–m* – discal medial crossvein; hum brk – humeral break; M_1 – first branch of media; m_1 – first medial cell; M_4 – fourth branch of media; m_4 – fourth medial cell; ptstg – pterostigma; r_1 – first radial cell; R_1 – anterior branch of radius; r_{2+3} – second + third radial cell; R_{2+3} – second branch of radius; r_{4+5} – fourth + fifth radial cell; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Rs* – radial sector; *sc* – subcostal cell; *Sc* – subcostal vein.

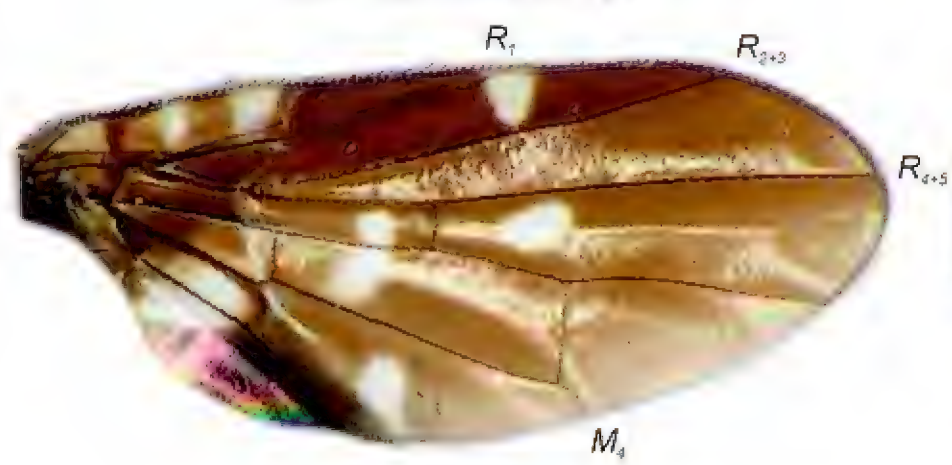
***Eosamphicnephes* Frey** (Platystomatinae)**.** An endemic monotypic genus, with the single described species, *E. africanus* Frey, 1932, with a disjunct distribution in Malawi and West Africa. Only two male specimens are known, of which one (a headless male), was examined in preparation of this chapter. The location of the second male specimen described by Frey was not established. The wing venation is reminiscent of *Oedemachilus* and the damaged specimen is only tentatively placed in the above identification key. No new material is known to exist. Biology and immature stages remain unknown.

***Eudasys* Whittington** (Plastotephritinae)**.** An endemic monotypic genus, with the single described species, *E. ophrys* Whittington, 2003 (Fig. 23), described from Central and West

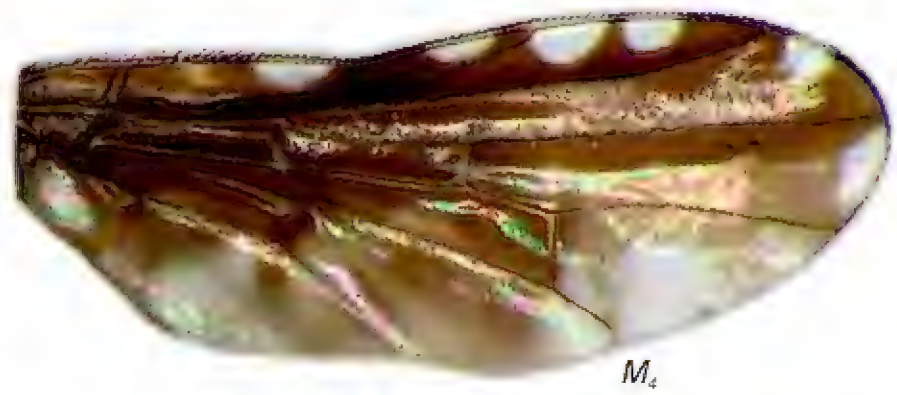
100 *Engistoneura* ♀



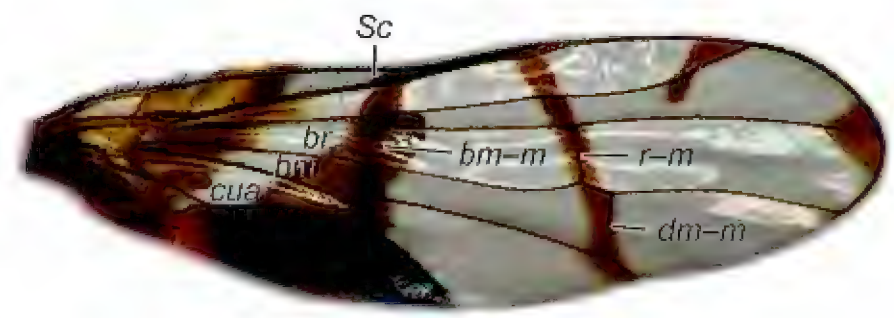
101 *Eudasys* ♂



102 *Federleyella* ♂

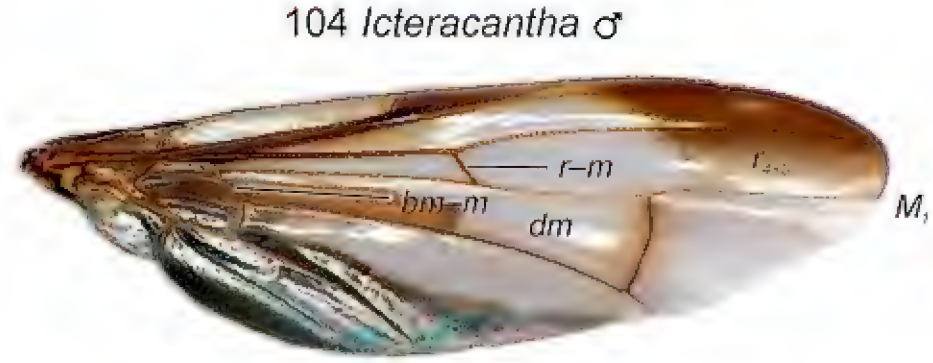


103 *Furcamyia* ♂

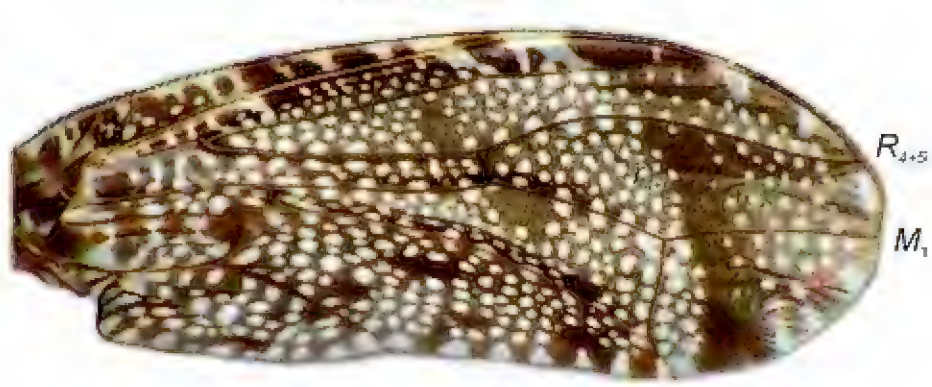


104 *Icteracantha* ♂

105 *Lambia* ♂



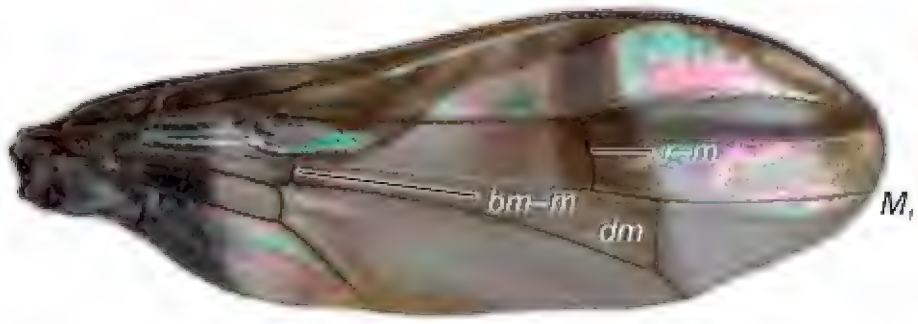
106 *Lamprophthalma* ♂



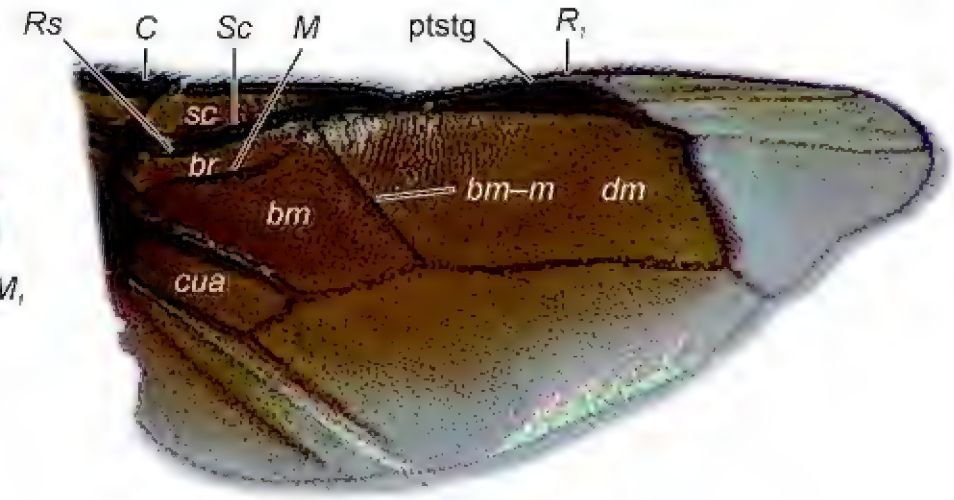
107 *Lophoplatystoma* ♀

Figs 70.100–107. Wings of Platystomatidae (dorsal views): (100) *Engistoneura moerens* (F.) ♀; (101) *Eudasys ophrys* Whittington ♂; (102) *Federleyella pallidipes* Whittington ♂; (103) *Furcamyia pallida* Whittington ♂; (104) *Icteracantha femorata* (Macquart) ♂; (105) *Lambia coelocephala* Hendel ♂; (106) *Lamprophthalma ochrifacies* Enderlein ♂; (107) *Lophoplatystoma molle* Hendel ♀. Fig. 101 (Whittington 2003, fig. 264).

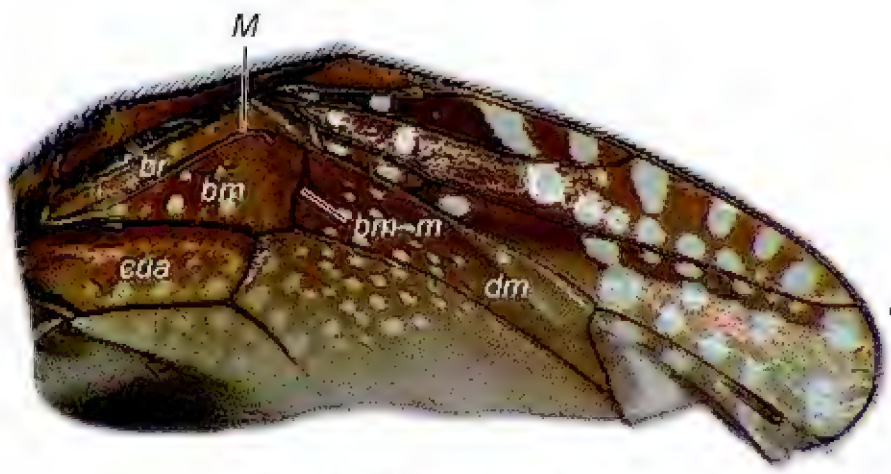
Abbreviations: *bm* – basal medial cell; *bm–m* – basal medial crossvein; *br* – basal radial cell; *cua* – anterior cubital cell; *dm* – discal medial cell; *dm–m* – discal medial crossvein; M_1 – first branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; r_{4+5} – fourth + fifth radial cells; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Sc* – subcostal vein.



108 *Loxoceromyia* ♂

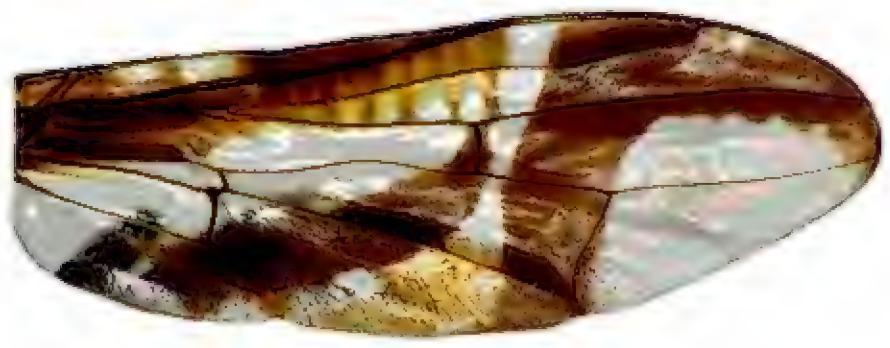


109 *Lule* ♀

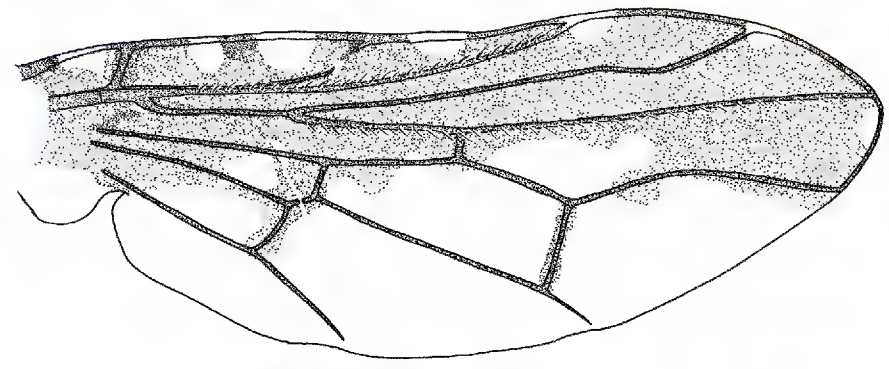


110 *Lulodes* ♀

111 *Mesanopin* ♀



112 *Mezona* ♀



113 *Micronesomyia* ♂

114 *Naupoda* ♂

115 *Neoardelio* ♀

Figs 70.108–115. Wings of Platystomatidae (dorsal views): (108) *Loxoceromyia longicornis* Hendel ♂; (109) *Lule corioptera* Speiser ♀; (110) *Lulodes seriatopunctatus* Enderlein ♀; (111) *Mesanopin tridens* Whittington ♀; (112) *Mezona proxenus* Speiser ♀; (113) *Micronesomyia hemihyalina* Whittington ♂; (114) *Naupoda inscripta* Speiser ♂; (115) *Neoardelio longiala* Steyskal ♀. Fig. 108 (© Trustees of Natural History Museum, London), Fig. 113 (Whittington 2003, fig. 440).

Abbreviations: *bm* – basal medial cell; *bm–m* – basal medial crossvein; *br* – basal radial cell; *C* – costal vein; *cua* – anterior cubital cell; *dm* – discal medial cell; *M* – medial vein, or media; M_1 – first branch of media; ptstg – pterostigma; R_1 – anterior branch of radius; r_{2+3} – second + third radial cell; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Rs* – radial sector; *sc* – subcostal cell; *Sc* – subcostal vein.

Africa. No undescribed species are currently known. *Eudasys* (Fig. 23) are small flies (body length: < 5 mm), with uniquely setulose dorsal lobes on the head (Fig. 69), setulose legs and a radiate wing pattern (Fig. 101). The genus shares an affinity with the Oriental genus *Agadasys* and is associated with other genera in the *Cladoderris*-group. The presence of a female aculeus that is oval in cross-section, with blunt cerci, bearing both lateral and ventral setulae suggests that eggs may be deposited on vegetation, rather than inserted into it. A male specimen collected while resting on fruits of *Syzygium jambos* L. Alston (Myrtaceae) implies that there may be a feeding or ovipositional association with fruit, possibly damaged by other insects. The genus appears to prefer woodland habitats. Biology and immature stages otherwise remain unknown. The species can be identified by reference to Whittington (2003).

Federleyella **Frey** (Plastotephritinae)**.** An endemic genus of two species, *F. pallidipes* (Enderlein, 1922) (Fig. 24) and *F. septemfenestrata* (Enderlein, 1922), which are widespread across Central, Southern and West Africa, as far south as Malawi and Zimbabwe, but apparently not east of the great lakes of the Albertine Rift. *Federleyella* are small flies (body length: < 4 mm), very similar in pattern (Figs 24, 102) and habitus to *Conopariella*. They clearly share a close affinity, but *Federleyella* may be distinguished by the bilobed median surstylus, with an outwardly directed hook midway along the stem, which articulates with a notch in the inner surface of the lateral surstylus. The female aculeus is also broad and flattened, with flat, apically acute cerci, bearing moderately long lateral setulae. They occur in a mixture of climax and secondary rainforest habitats and in riparian forest and vegetation. Biology and immature stages otherwise remain unknown. An identification key to the two species was provided by Whittington (2003).

Furcamyia **Whittington** (Plastotephritinae)**.** An endemic genus of four species (Fig. 25), predominantly distributed in isolated centres in East, Southern and West Africa. Given the few specimen records this information is derived from, the apparent distribution may be a collecting artefact of a much more widely distributed genus. Species are small (body length: < 5 mm), with a combination of yellow and dark brown colouration (Figs 25, 103), that makes them difficult to locate in their preferred dense forest habitats. *Furcamyia gladiatura* Whittington, 2003, is the only plastotephritine known from Afromontane mist-belt *Podocarpus* forest. Representatives of the genus tend to hold the abdomen upright at a slanting angle. The presence of sexual dimorphism in the form of slight expansion of the genae, on the one hand, and well-developed ventral spines on the fore femora on the other, makes the affinities of the genus difficult to interpret, but it may straddle the *Conopariella*/*Federleyella* and *Agrochira*/*Mesanopin* genus-groups. The female aculeus is rigid, with flat, apically acute cerci bearing moderately long lateral setulae, suggesting oviposition between tightly appressed plant axils, but no detailed observations have been made to substantiate this. Biology and immature stages otherwise remain unknown. An identification key to the four species was provided by Whittington (2003).

Icteracantha **Hendel** (Platystomatinae)**.** A genus of four described species, occurring in the Afrotropical and Oriental Regions. The single Afrotropical species, *I. femorata* (Macquart, 1843) (Figs 26, 104), is confined to Madagascar and Réunion Is. in the Indian Ocean. No additional undescribed species are known. It is a distinctive genus with the femora with rows of ventral spines (Figs 147, 148). Biology and immature stages remain unknown.

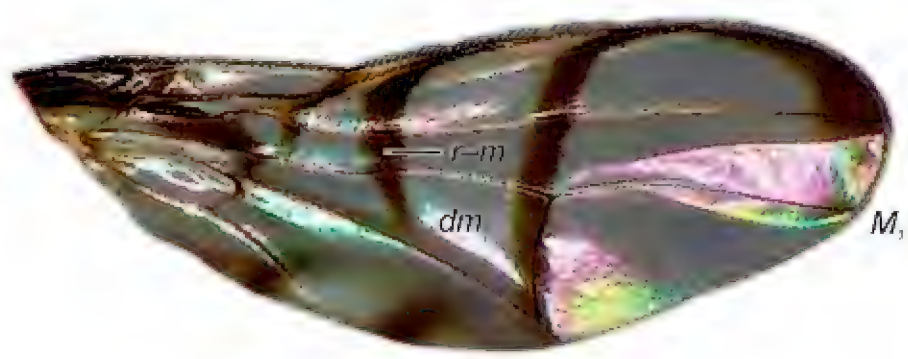
Lambia **Hendel** (Platystomatinae)**.** An endemic, currently monotypic genus, with the single described species, *L. coelocephala* Hendel, 1914 (Fig. 27), recorded from Mozambique and Tanzania. One additional undescribed species is known from Kenya. It is a highly distinctive genus, with the frons concave, the antennae inserted dorsal to the middle of the compound eye (Fig. 27), wing crossveins *r–m* and *dm–m* coincident (Fig. 105) and the fore femur setose ventrally (Fig. 152). Biology and immature stages remain unknown. Revision of the genus is needed and no identification key to species is currently available.

Lamprophthalma **Portschinsky** (Platystomatinae)**.** A genus of 15 described species occurring in the Afrotropical, Oriental and Palaearctic Regions. Three species are recorded from the Afrotropics: *L. ochrifacies* Enderlein, 1924 (Fig. 28), from Cameroon and Equatorial Guinea; *L. rufoscutellata* Hendel, 1914, from Cameroon, Democratic Republic of Congo and Zimbabwe; and *L. togoensus* Enderlein, 1924, from Togo. No additional undescribed species are known. These flies superficially resemble *Plagiostenopterina*, from which they can be distinguished by the absence of postpronotal setae; the frons and ocellar triangle are tuberculate (Fig. 67), creating a central "dimple" on the frons in front of the ocellar triangle; wing cell r_{4+5} is not narrowed toward the apex, crossvein *bm–m* is noticeably oblique (Fig. 106); and the wings are sometimes folded in half lengthwise at rest. Nothing is known of the habitat preferences or biology and immature stages remain unknown. Revision of the genus is needed and no identification key to species is currently available.

Lophoplatystoma **Hendel** (Platystomatinae)**.** An endemic genus of five described species (Fig. 29), distributed in East and West Africa, southwards to South Africa. No additional undescribed species are known. These flies superficially resemble the genus *Peltacanthina*, but are distinguished from it by the lack of tubercles at the bases of scutellar setae and in having the body and wings distinctly maculate (grey or brown) (Figs 29, 107); they are very similar to Palaearctic species of the genus *Platystoma*, in having the head and body microtrichia forming a reticulate pattern, the scutellum with three pairs of sessile marginal setae and cell r_{4+5} widened medially, differing in having the arista plumose (short-pubescent in *Platystoma*). Little is known of the habitat preferences or biology, but Speiser (1914) recorded *L. leucolena* Speiser, 1914, from high elevations (800–2,100 m) in Cameroon. Revision of the genus is needed and no identification key to species is currently available.

Loxoceromyia **Hendel** (Platystomatinae)**.** An endemic monotypic genus, with the single described species, *L. longicornis* Hendel, 1914, described from Ghana (Figs 30, 108). No additional undescribed species are known. Nothing is known of the habitat preferences or biology of the species and immature stages remain unknown.

Lule **Speiser** (Trapherinae)**.** The largest trapherine genus of ten described species (Fig. 31), occurring in the Afrotropical

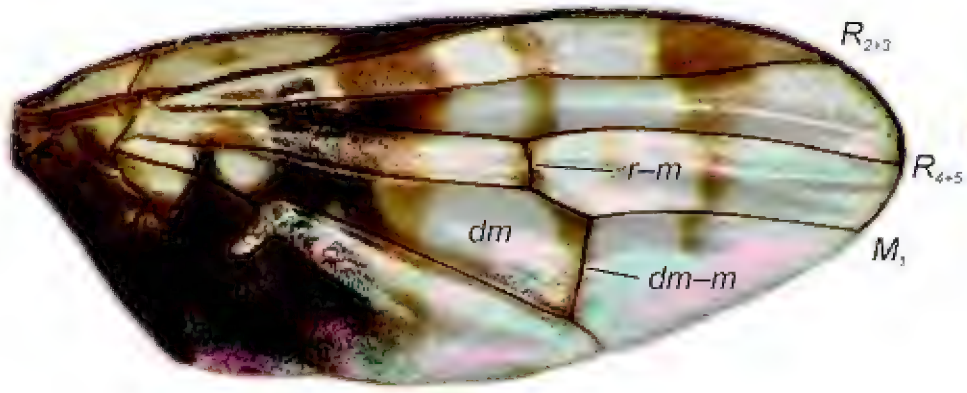


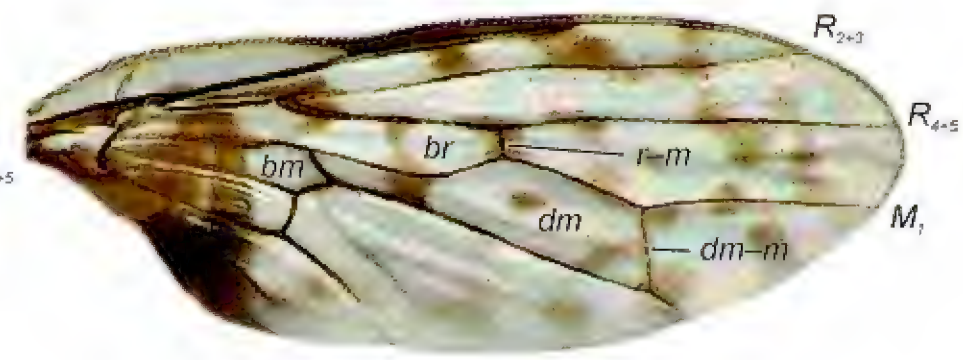
116 *Neoepidesma* ♀

117 *Oeciotypa* ♂

118 *Oedemachilus* ♂

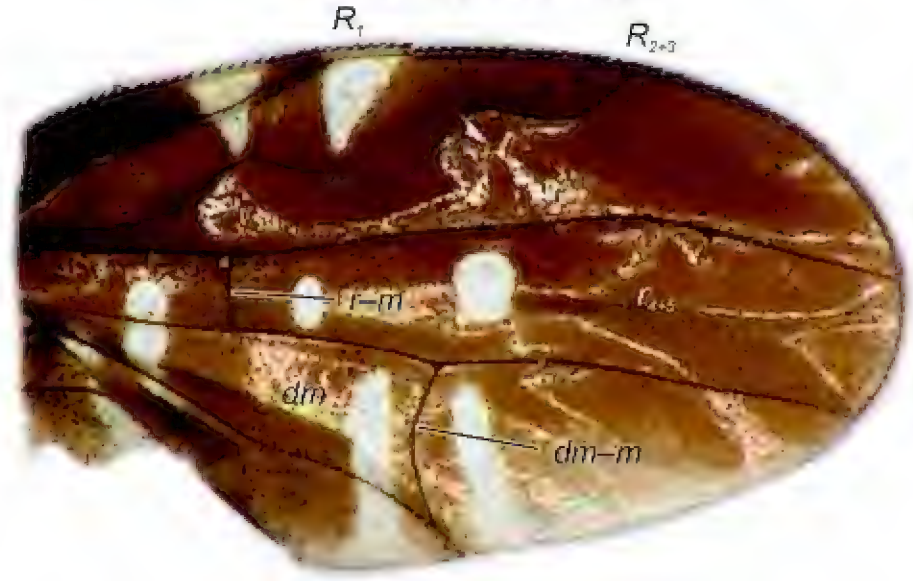
119 *Palpomya* ♀





121 *Paryphodes* ♀

120 *Parardelio* ♀



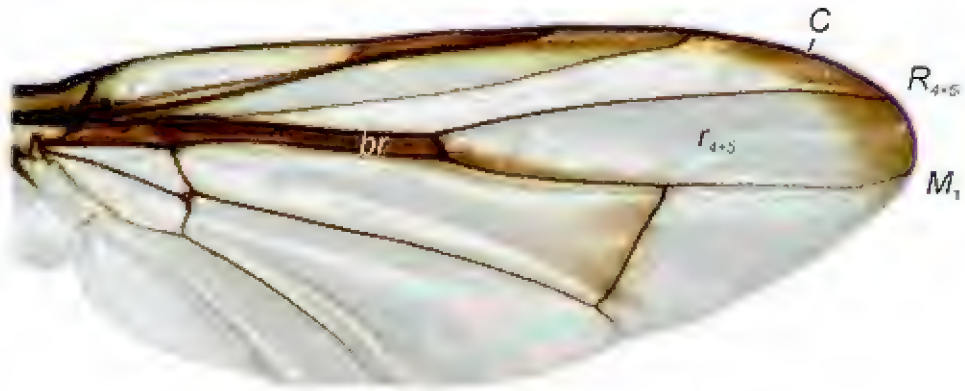
122 *Peltacanthina* ♀

123 *Phlebophis* ♀

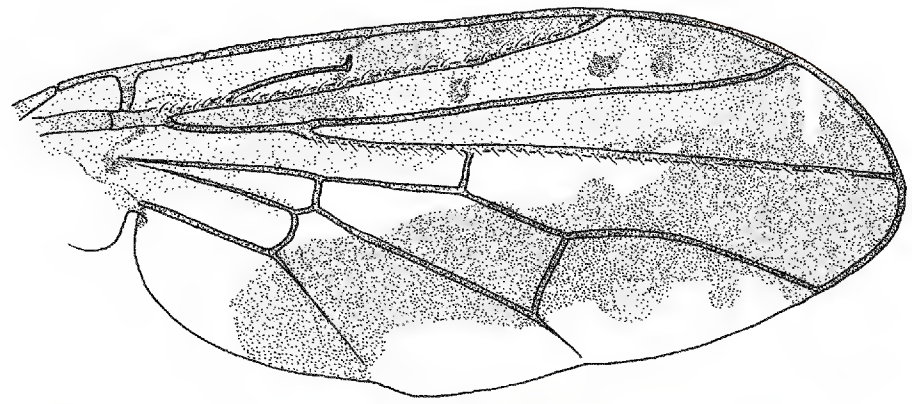
Figs 70.116–123. Wings of Platystomatidae (dorsal views): (116) *Neoepidesma thoracale* Hendel ♀; (117) *Oeciotypa hendeli* Lindner ♂; (118) *Oedemachilus coquereli* Bigot ♂; (119) *Palpomya asphaltina* (Wiedemann) ♀; (120) *Parardelio voeltzkowi* Enderlein ♀; (121) *Paryphodes neptiluca* (Loew) ♀; (122) *Peltacanthina* sp. ♀; (123) *Phlebophis serpentina* Frey ♀.

Abbreviations: *bm* – basal medial cell; *br* – basal radial cell; *dm* – discal medial cell; *dm–m* – discal medial crossvein; M_1 – first branch of media; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; r_{4+5} – fourth + fifth radial cells; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein.

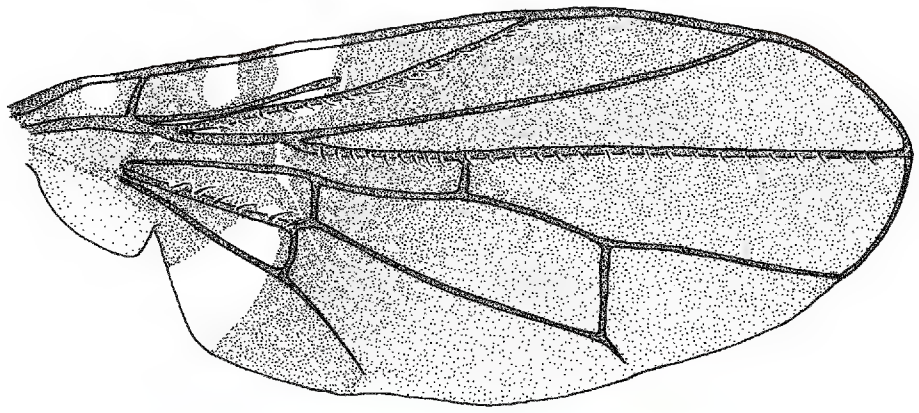
124 *Phytalmodes* ♀



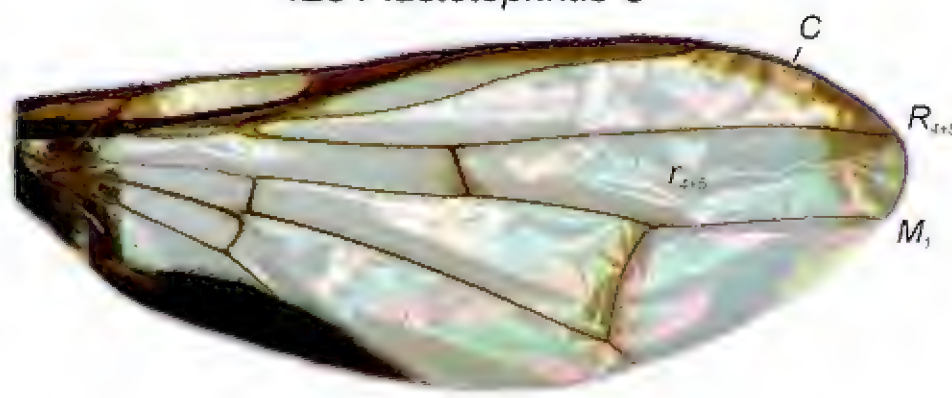
125 *Plagiostenopterina* ♂



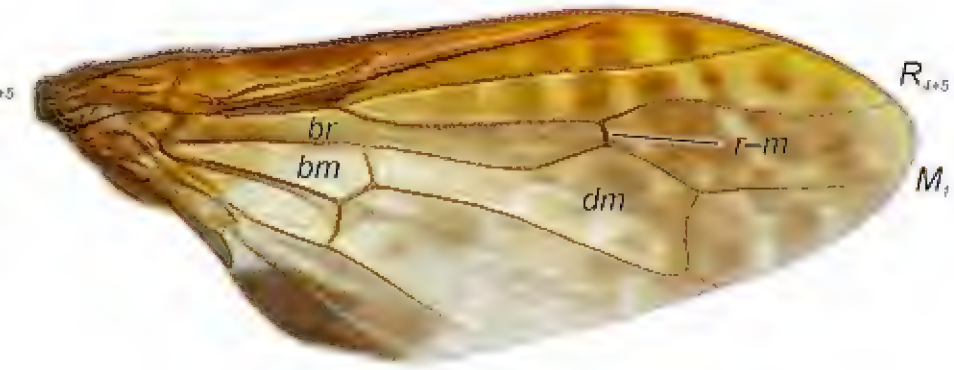
126 *Plastotephritis* ♂



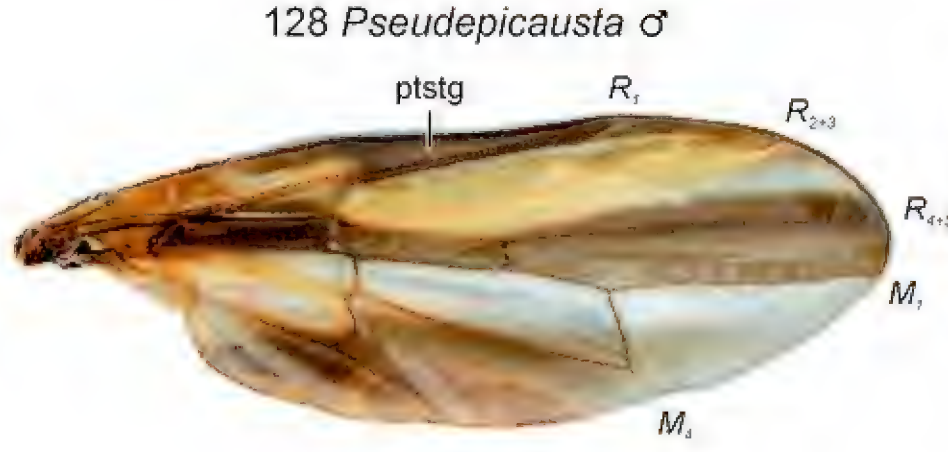
127 *Prosopoconus* ♂



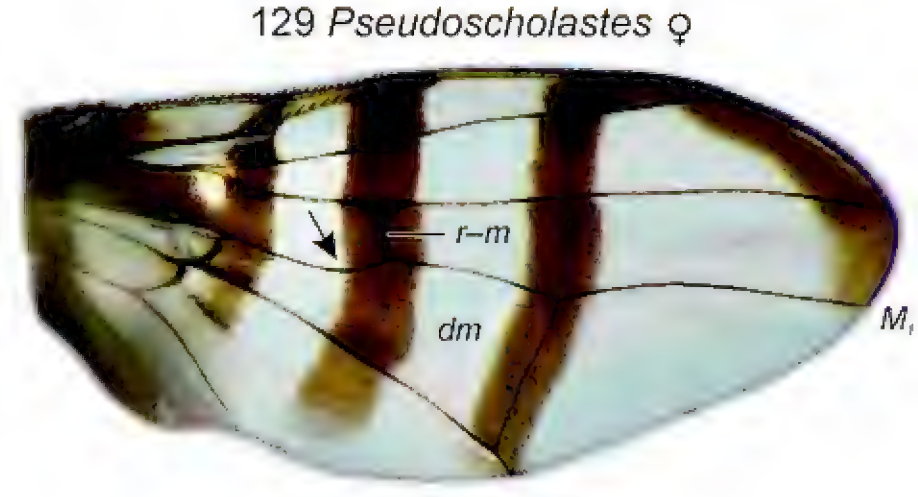
128 *Pseudepicausta* ♂



129 *Pseudoscholastes* ♀



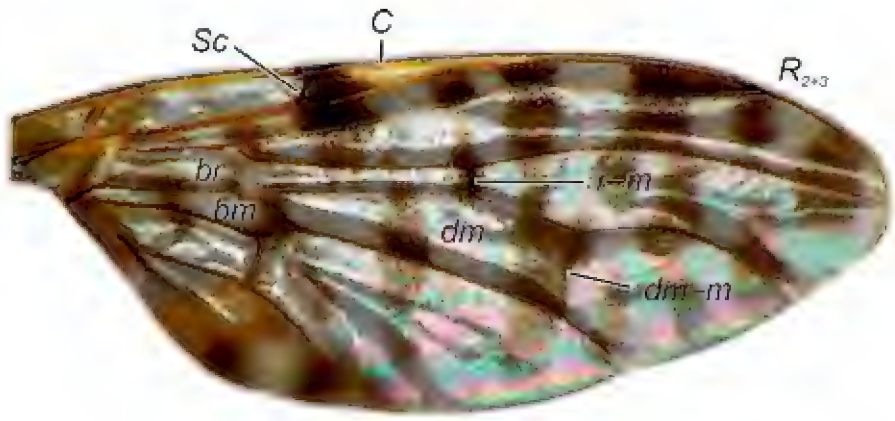
130 *Pterogenomyia* ♀



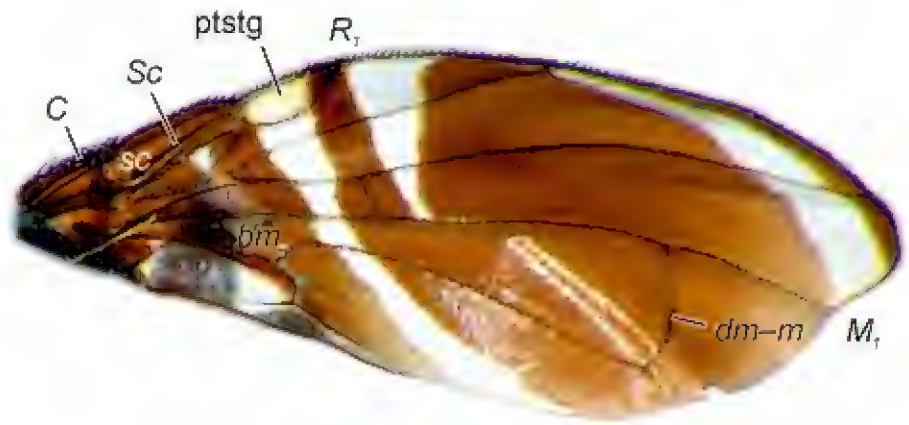
131 *Rivellia* ♂

Figs 70.124–131. Wings of Platystomatidae (dorsal views): (124) *Phytalmodes africanus* Bezzi ♀; (125) *Plagiostenopterina* sp. ♂; (126) *Plastotephritis sica* Whittington ♂; (127) *Prosopoconus fuscigenu* Enderlein ♂; (128) *Pseudepicausta* sp. ♂; (129) *Pseudoscholastes marshalli* Frey ♀; (130) *Pterogenomyia picta* (Bigot) ♀; (131) *Rivellia* sp. ♂ (arrow indicates dip of vein M_1 into cell *dm*). Figs 126, 127 (Whittington 2003, figs 522, 531), Fig. 130 (© Royal Museum for Central Africa).

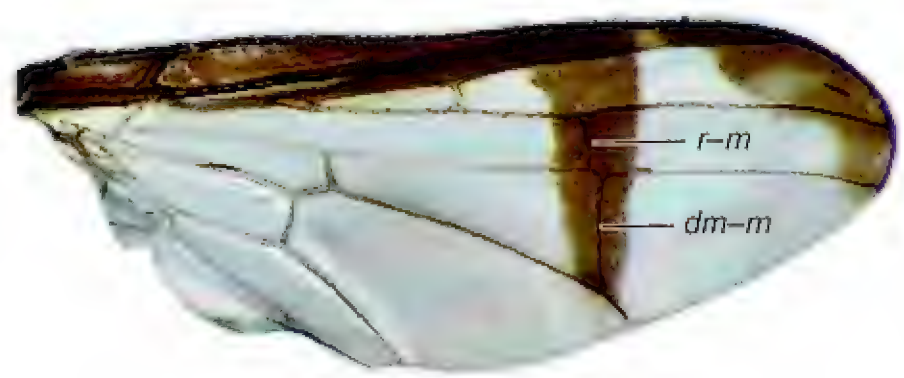
Abbreviations: *bm* – basal medial cell; *br* – basal radial cell; *C* – costal vein; *dm* – discal medial cell; *dm–m* – discal medial crossvein; M_1 – first branch of media; M_4 – fourth branch of media; ptstg – pterostigma; r_1 – first radial cell; R_1 – anterior branch of radius; r_{2+3} – second + third radial cell; R_{2+3} – second branch of radius; r_{4+5} – fourth + fifth radial cells; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein.



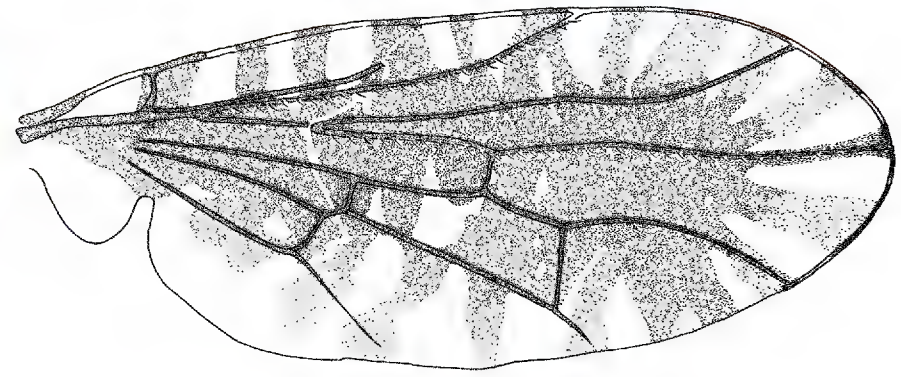
132 *Scholastes* ♀



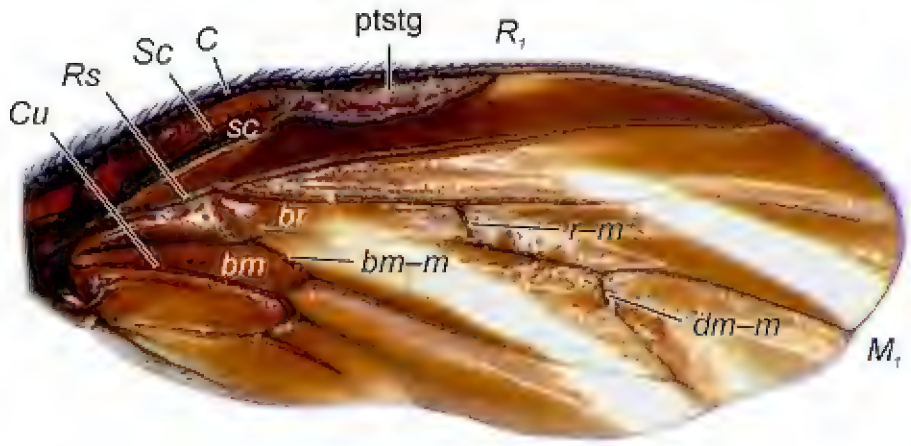
133 *Seguyopiara* ♀



134 *Sphenoprosopa* ♂



135 *Stellapteryx* ♂



136 *Traphera* ♂

137 *Venacalva* ♂

138 *Xyrogena* ♀

Figs 70.132–138. Wings of Platystomatidae (dorsal views): (132) *Scholastes vicarius* Hendel ♀; (133) *Seguyopiara* sp. ♀; (134) *Sphenoprosopa fascipennis* Macquart ♂; (135) *Stellapteryx stellata* Whittington ♂; (136) *Traphera chalybea* Wiedemann ♂; (137) *Venacalva virga* Whittington ♂; (138) *Xyrogena gratiosa* (Enderlein) ♀. Fig. 135 (Whittington 2003, fig. 556).

Abbreviations: *bm* – basal medial cell; *bm–m* – basal medial crossvein; *br* – basal radial cell; *C* – costal vein; *Cu* – cubital vein or cubitus; *dm* – discal medial cell; *dm–m* – discal medial crossvein; M_1 – first branch of media; M_4 – fourth branch of media; ptstg – pterostigma; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; *r–m* – radial–medial crossvein; *Rs* – radial sector; *sc* – subcostal cell; *Sc* – subcostal vein.

and Oriental Regions. Eight species occur in the Afrotropics, distributed in Central, East and Southern Africa and in Madagascar. Several undescribed species are known from Angola, Democratic Republic of Congo and Uganda. *Lule* is a conspicuously distinctive genus (Fig. 31), with short wings, bearing unusually enlarged wing cells *bm* and *dm*, such that cell *br* is constricted by the proximity of the radial sector (*Rs*) and the medial vein (*M*) (Fig. 109). There are strong similarities with the wing venation in *Naupoda* and the two genera can be readily separated by the plumose arista in *Lule*, but bare arista in *Naupoda*. Given the separate subfamily placements, it is likely that functional convergence is exhibited in the wing venation, rather than a true phylogenetic relationship. Furthermore, given the range of variation within wing venation characters observed in specimens examined (including potential new species), the key character used by Steyskal (1990) to distinguish *Microlule* Steyskal (apical angle of *bm* < 90°), is probably not a valid autapomorphy. The result is that the single species *M. flavimana* Steyskal, 1990 from South Africa is included here in *Lule*. Speiser (1910) recorded *L. corioptera* Speiser, 1910, from elevations of 1,300–1,900 m on Mt Kilimanjaro in Tanzania, but nothing is known of the biology and immature stages of the other species in the region. An identification key to Afrotropical species was provided by Steyskal (1960: 315), but *L. cyanea* Enderlein, 1912 from Madagascar was omitted and the genus requires revision and a new identification key.

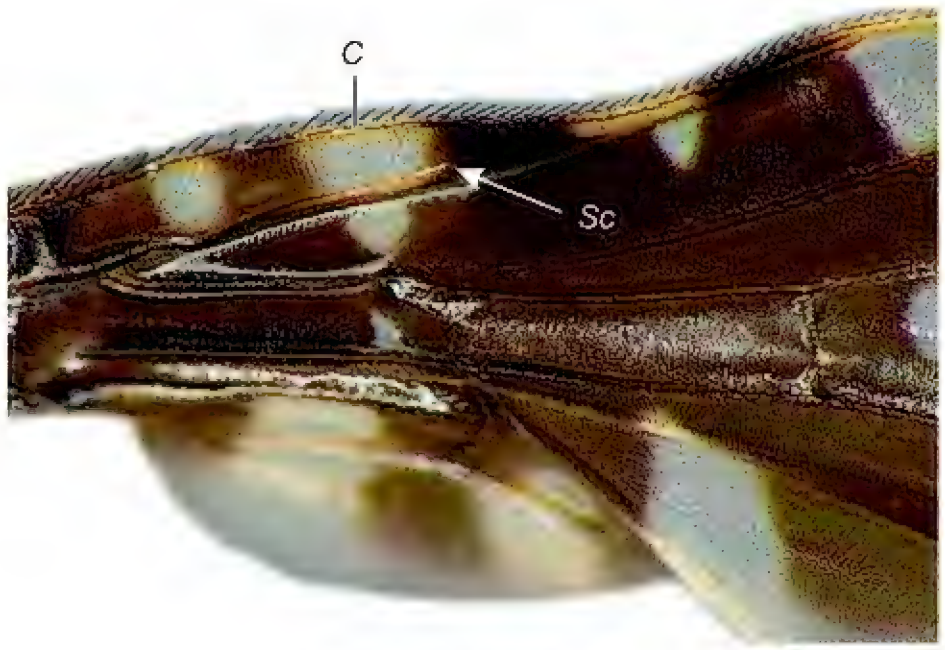
***Lulodes* Enderlein** (Platystomatinae)**.** An endemic genus of two described species: *L. asteropterus* (Frey, 1924), described from Nigeria; and *L. seriatopunctatus* Enderlein, 1924 (Fig. 32), from Central, East and West Africa. No additional undescribed species are known. An unusual genus, having the wing venation reminiscent of *Lule* and *Naupoda*, suggesting its placement in the Platystomatinae may be questionable. It is distinctive, without orbital setae; wing cell *bm* is almost triangular, considerably wider at the apex than at the base (Fig. 110); cell *dm* is rectangular and virtually parallel-sided; and the wing membrane has blister-like hyaline maculae. Biology and immature stages remain unknown. Revision of the genus is needed and no identification key to species is currently available.

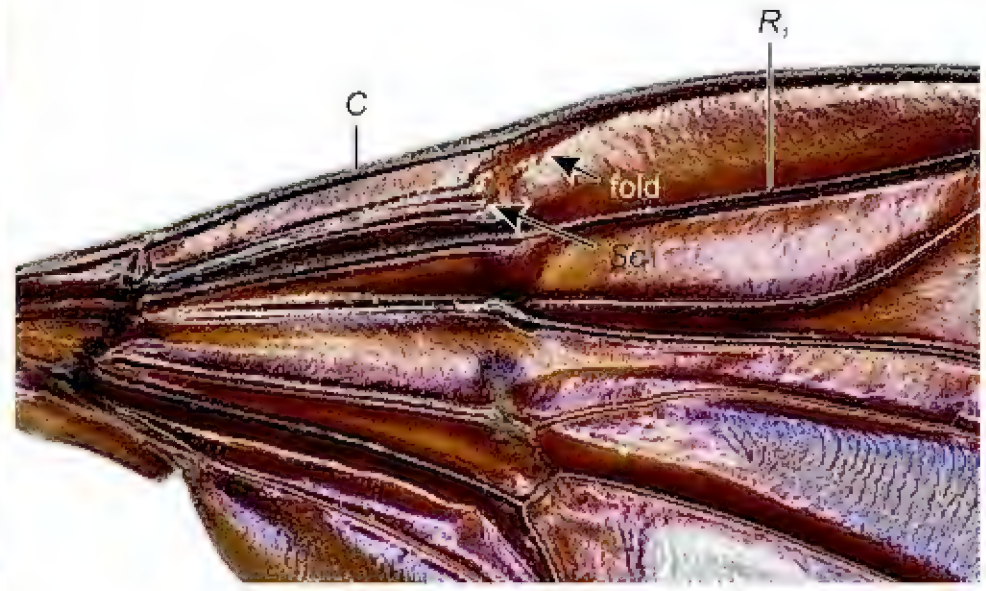
***Mesanopin* Enderlein** (Plastotephritinae)**.** An endemic genus of 14 described species (Figs 33, 111), restricted to the continental Afrotropics and widely distributed across Central, East, Southern and West Africa. At least one additional undescribed species is known from Togo. Additional sampling is required, as the combination of maculate wings and body pattern make representatives of the genus cryptic in their natural habitat of lowland forest, scrubland and Afromontane forest. The drier habitat preference may preclude the genus from the more mesic parts of tropical Africa and they sometimes occur in agricultural lands. Species are small (commonly body length: < 5 mm), with yellow and brown bodies and distinctively dark brown wings, marked with scattered hyaline maculae (Fig. 33). They are sexually dimorphic, with males having stout spines on the ventral surface of the fore femora (Fig. 146) and although moderate expansion of the parafacial area is apparent in some species, the development of eye stalks (as expressed in *Agrochira*), is not. The female aculeus is wide oval in cross-section, with blunt, ovoid cerci, bearing both lateral and ventral setulae (Fig. 161), suggesting that eggs may be deposited in a variety of substrates. *Mesanopin* shares a close affinity with *Agrochira*, another genus endemic to the region. Biology and immature stages otherwise remain unknown. An identification key to the 14 species was provided by Whittington (2003).

***Mezona* Speiser** (Platystomatinae)**.** An endemic genus of three described species: *M. compta* (Enderlein, 1912), described from Tanzania; *M. mwinilungae* Hancock, 1987, from Zambia; and *M. proxenus* Speiser, 1910, from Tanzania (Fig. 34). An additional three undescribed species are known from Democratic Republic of Congo, Malawi, Tanzania and Zimbabwe. To some extent species resemble central Asian *Steyskaliella* Soós, *Engistoneura* and some *Peltacanthina*. Representatives of the genus are distinguishable from *Steyskaliella* and *Engistoneura* by the antennal insertions being separated by less than the width of the antennal scape, by possessing one pair of vertical setae (Fig. 66) and from *Peltacanthina* by the scutellum, which lacks tubercles at the base of the scutellar setae. In addition, similarly to *Steyskaliella*, *Mezona* has elongate wings (Figs 34, 112), less densely patterned than those of *Engistoneura*, usually with narrow brown bars or maculae. Speiser (1910) recorded *M. proxenus* from elevations of 1,300–1,900 m on Mt Kilimanjaro in Tanzania and one of the species awaiting description is from Afromontane forest between 1,500 and 1,650 m on Mt Selinda in Zimbabwe and the Ntchisi Forest in Malawi. Most of the type series of *M. mwinilungae* was collected from butterfly traps baited with fermenting fruit. Biology and immature stages otherwise remain unknown. Revision of the genus is needed and no identification key to species is currently available.

***Micronesomyia* Whittington** (Plastotephritinae)**.** An endemic monotypic genus, with the single described species, *M. hemihyalina* Whittington, 2003, confined to Madagascar. No additional undescribed species are known. A small-sized (body length: < 5 mm), predominantly pale cream coloured species, with brown markings and the anterior half of the wing membrane brown and the posterior half hyaline (Fig. 113). Affinities are difficult to establish in this geographically isolated species, but shared characteristics suggest that it may be a representative of the *Agrochira*-group. The species is not sexually dimorphic, suggesting it may be closer to *Furcamyia* than to either *Agrochira* or *Mesanopin*. Noticeably, the hind trochanter and tibia are modified in a manner not dissimilar to *Xyrogena*, making the placement of this species in a specific group problematical. The female aculeus is soft, almost round in cross-section, bearing ovoid cerci with moderately long dorsolateral and ventrolateral setulae and not at all robust, suggesting eggs are deposited into soft substrates, possibly into holes or cracks in fallen fruits. Biology and immature stages otherwise remain unknown. The species can be identified by reference to Whittington (2003).

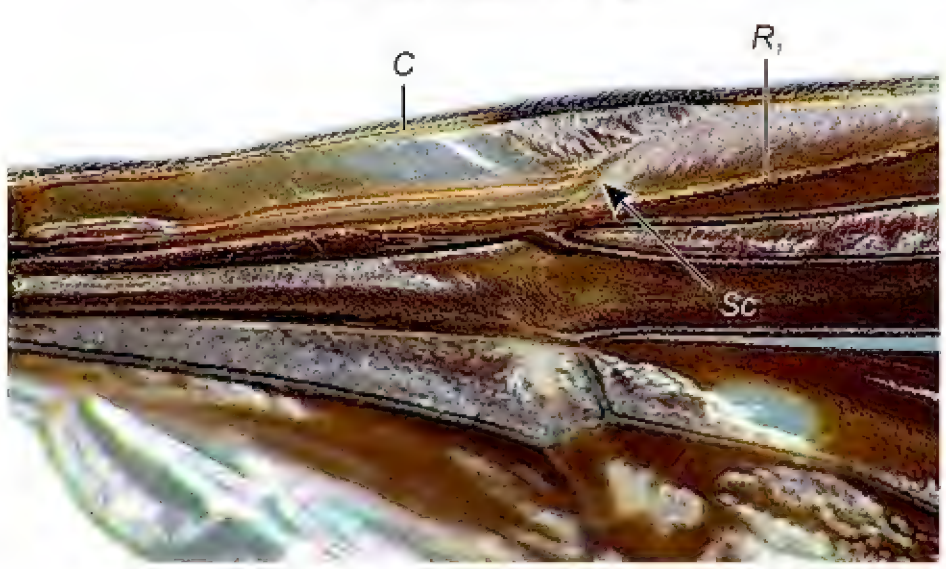
***Naupoda* Osten-Sacken** (Scholastinae)**.** A genus of 19 species occurring in the Afrotropical, Australasian and Oriental Regions. Eight species occur in the Afrotropics, distributed across East, Southern and West Africa. Two possibly undescribed species are known from Uganda. The compact body form and head closely associated to the body, partly folded wings and the distinctive wing venation make the genus unmistakable (Figs 6, 35, 36, 114). Note that contrary to the subfamily characteristics, the katepisternal seta is absent and the similarity with *Lule* in the unusual wing venation is discussed

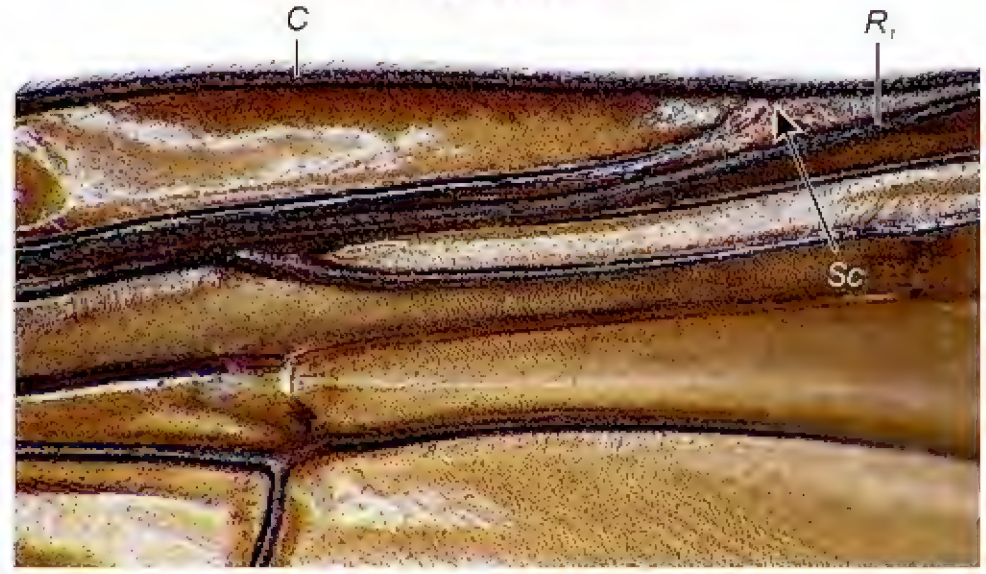




139 *Conopariella* ♀

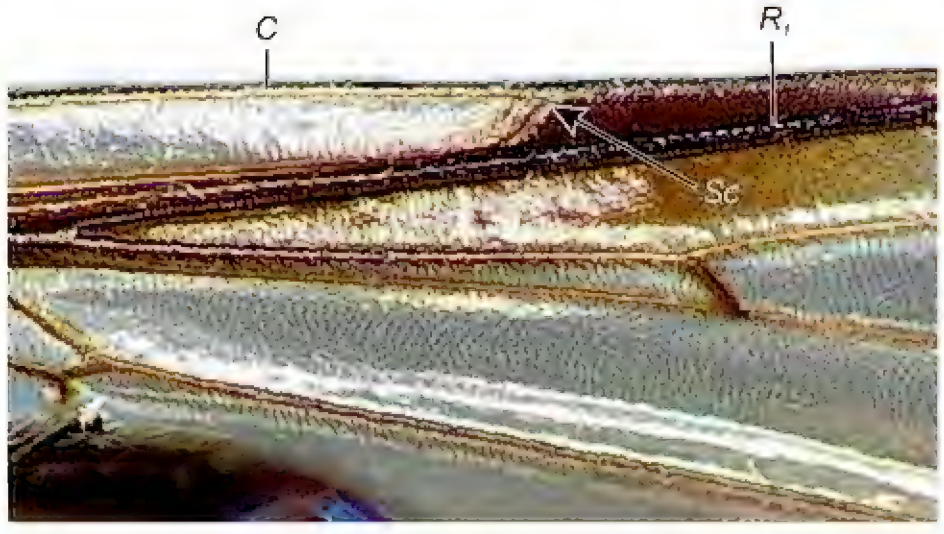
140 *Clitodoca* ♂

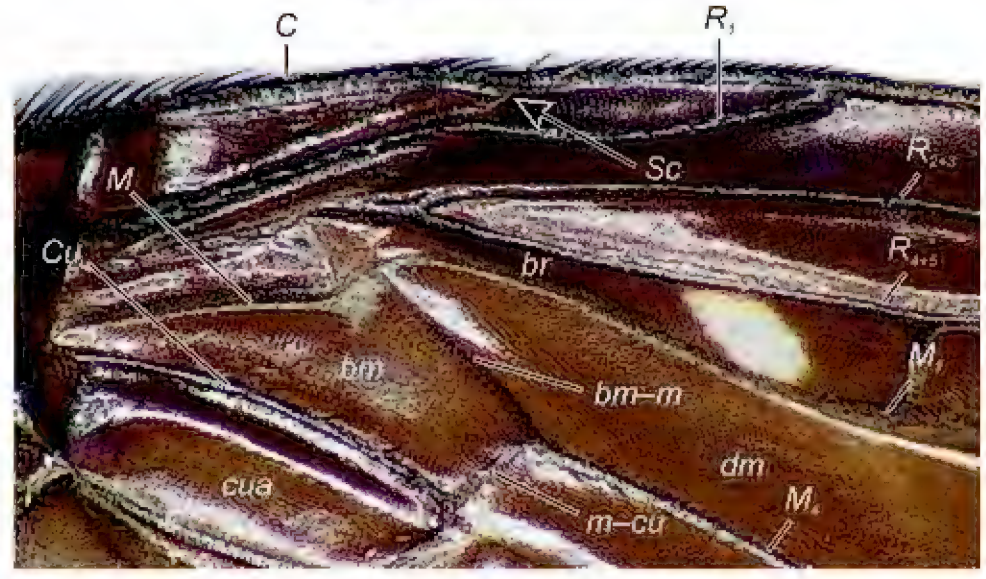




141 *Phytalmodes* ♀

142 *Bromophila* ♂





143 *Lamprophthalma* ♂

144 *Traphera* ♂

Figs 70.139–144. Details of wing venation of Platystomatidae (dorsal views; arrows indicate terminal point of subcostal vein (*Sc*)): (139) *Conopariella tibialis* (Hendel) ♀; (140) *Clitodoca fenestralis* (Macquart) ♂; (141) *Phytalmodes africanus* Bezzi ♀; (142) *Bromophila caffra* (Macquart) ♂; (143) *Lamprophthalma ochrifacies* Enderlein ♂; (144) *Traphera chalybea* Wiedemann ♂.

Abbreviations: *bm* – basal medial cell; *bm–m* – basal medial crossvein; *br* – basal radial cell; *C* – costal vein; *Cu* – cubital vein or cubitus; *cua* – anterior cubital cell; *dm* – discal medial cell; *M* – medial vein, or media; M_1 – first branch of media; M_4 – fourth branch of media; *m–cu* – medial–cubital crossvein; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *Sc* – subcostal vein.

under that genus. Frey (1932) recorded *N. hemiptera* Frey, 1932 on inflorescences of *Terminalia catappa* L. (Combretaceae) and Speiser (1910) recorded *N. inscripta* Speiser, 1910, from elevations of 1,000–1,200 m on Mt Kilimanjaro in Tanzania. Frey (1932) recorded *N. nyasica* at an elevation of 870 m. Some specimens of a species near *N. nyasica* Frey, 1932 were reared from larvae scavenging in galleries of the platypodid weevil, *Trachyostus schaufussi* Schedl (Curculionidae) in logs of *Celtis mildbraedii* Engl. (Cannabaceae) in lowland rainforest in Nigeria (Roberts 1969). Biology and immature stages otherwise remain unknown. Revision of the genus is needed and no identification key to species is currently available.

***Neoardelio* Hendel** (Platystomatinae)**.** An endemic genus of six described species (Fig. 37), distributed south of the Kunene and Zambezi Rivers in Southern Africa. At least one additional undescribed species is known from South Africa. *Neoardelio* is one of a cluster of genera centred on *Rivellia* and most closely aligned with *Neoepidesma*, from which it is distinguished in having a reduced anterior orbital seta, no ventral setae on the fore femur, two pairs of scutellar marginal setae (as opposed to one pair in *Neoepidesma*) and wing vein M_1 straight to slightly curved (Fig. 115), not distinctly bowed into cell *dm* proximal to *r–m*, as is the case in *Neoepidesma* (compare Fig. 116). Species are small (commonly body length: 3–4 mm). The notum is frequently distinctively marked by microtrichia and distinctive patterns of microtrichia are present on the anepisternum. Species occur at an elevational range from 100–2,000 m, in vegetation types ranging from semi-arid farmland, through grassland to sub-tropical vegetation. Information concerning larval habitats is rudimentary at best, although *N. aspalathus* and *N. lineatocollis* are both possibly associated with the root nodules of the Rooibos tea plant, *Aspalathus linearis* (Burman f.) Dahlgren (Fabaceae). Biology and immature stages otherwise remain unknown. The genus was revised by Whittington (2000*b*), who provided an identification key to the six species.

***Neoepidesma* Hendel** (Platystomatinae)**.** An endemic genus of eight described species (Fig. 38), distributed in East and Southern Africa. No additional undescribed species are known. *Neoepidesma* is one of a cluster of genera centred on *Rivellia*. The genus can be distinguished from *Neoardelio* and *Rivellia*, in having a single pair of orbital setae positioned forward of the anterior ocellus (Fig. 77); only one pair of long apical marginal scutellar setae (noticeably long, reaching beyond posterior margin of syntergite 1 + 2), in having wing vein M_1 distinctly bowed into cell *dm* proximal to crossvein *r–m* (Fig. 116) and the fore femur with ventral setae (the last two mentioned features shared with *Rivellia*, but not with *Neoardelio*). Biology and immature stages remain unknown. Steyskal (1964) provided an identification key to species.

***Oeciotypa* Hendel** (Plastotephritinae)**.** An endemic genus of six described species, occurring throughout the continental Afrotropics. The genus is more widely distributed than other Afrotropical representatives of the Plastotephritinae. No additional undescribed species are known. Small-sized (body length: < 4 mm), distinctive species, with entirely black bodies, with white pruinose patterns, a heavily sclerotised convex abdomen (Figs 7, 39) and barred wing patterns (Fig. 117). The female aculeus is virtually round in cross-section, bearing the ovoid cerci with moderately long dorsolateral and ventrolateral setulae, suggesting eggs may be deposited into cracks or crevices in the substrate. Exceptionally, the subcostal vein (*Sc*) is not distinctly bent toward the costal vein (*C*). This, and the hardened abdominal tergites, led Frey (1932) to postulate that the genus approaches the typical form of Platystomatinae, but there is no further evidence suggesting that the genus does not belong in the Plastotephritinae. There is, however, no shared affinity with other genera within the latter subfamily, thus the genus appears to be an isolated lineage. Frey (1932) recorded *O. rotundiventris* Frey, 1932 at an elevation of 1,330 m in Malawi. Biology and immature stages otherwise remain unknown. An identification key to the six species was provided by Whittington (2003).

***Oedemachilus* Bigot** (Platystomatinae)**.** An endemic monotypic genus, with the single described species, *O. coquereli* Bigot, 1860 (Fig. 40), confined to Madagascar. An additional undescribed species is known from Madagascar. The genus is distinctive in having crossveins *r–m* and *dm–m* closer together than the length of either crossvein (Fig. 118) and the apex of the wing has a distinctive inverted V-shaped pattern. Biology and immature stages remain unknown. Revision of the genus is needed and an identification key to species is currently unavailable.

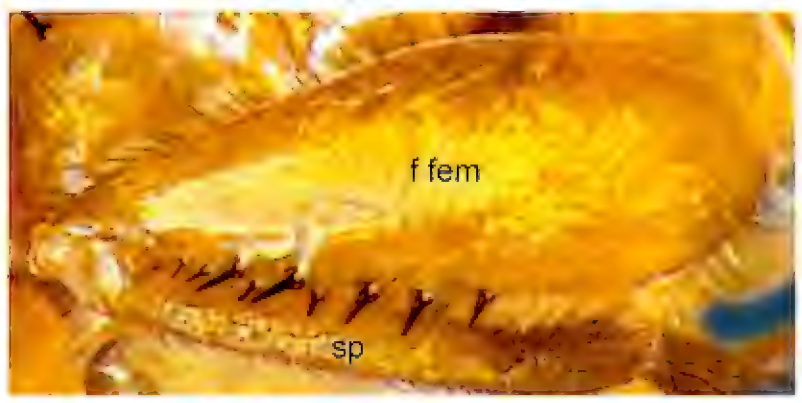
***Palpomya* Robineau-Desvoidy** (Platystomatinae)**.** An endemic genus of six described species (Fig. 41), distributed in East and Southern Africa. One additional undescribed species is known from Democratic Republic of Congo. Medium- to large-sized flies, body length > 6 mm (7–12 mm). The noticeably enlarged lower calypter (Fig. 91) sets the genus apart from others with a similar general habitus, such as *Lophoplatystoma* and *Peltacanthina*. The generally black body colour and wing (Figs 41, 119) resemble *Bromophila*, from which it can be distinguished by the presence of ocelli and the elongate lower calypter. Biology and immature stages remain unknown. Revision of the genus is needed and an identification key to species is currently unavailable.

***Parardelio* Hendel** (Scholastinae)**.** An endemic genus of two species: *P. pilosus* Hendel, 1912, described from Seychelles; and *P. voeltzkowi* Enderlein, 1924 (Fig. 42), from Madagascar. No additional undescribed species are known. The antennal arista is pubescent and the frons is strongly curved and narrows strongly toward the vertex (in frontal view) (Fig. 70), distinguishing the genus from *Paryphodes*. In keeping with the subfamily characteristics, a katepisternal seta is present, inserted at the posterodorsal margin. To some extent specimens assigned to the genus resemble *Paryphodes*, or miniature *Scholastes*, but are easily distinguished by the short, non-seriate branches on the arista, two pairs of orbital setae (Fig. 78) and wing vein R_{2+3} straight (Fig. 120). Both sexes of an unidentified species of *Parardelio* were found resting on bananas in Madagascar and *P. pilosus* was collected at elevations between 240–450 m in Seychelles (Whittington 2009: 316). Biology and immature stages otherwise remain unknown. Revision of the genus is needed and an identification key to species is currently unavailable.

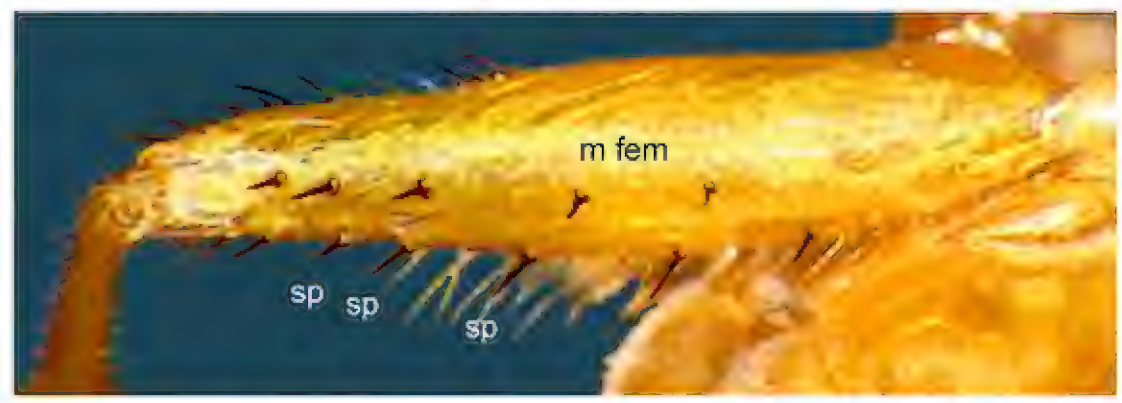
***Paryphodes* Speiser** (Scholastinae)**.** An endemic genus of 17 described species (Fig. 43), widely distributed in the continental Afrotropics and Bioko Is. (Equatorial Guinea). At least one undescribed species is known from South Africa. As with *Parardelio*, species assigned to the genus resemble miniature

145 *Agrochira* ♂

146 *Mesanopin* ♀

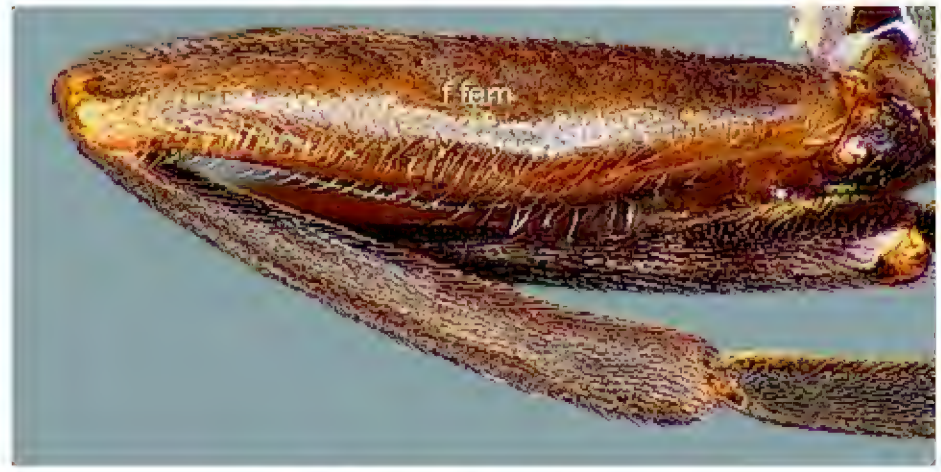


147 *Icteracantha* ♂

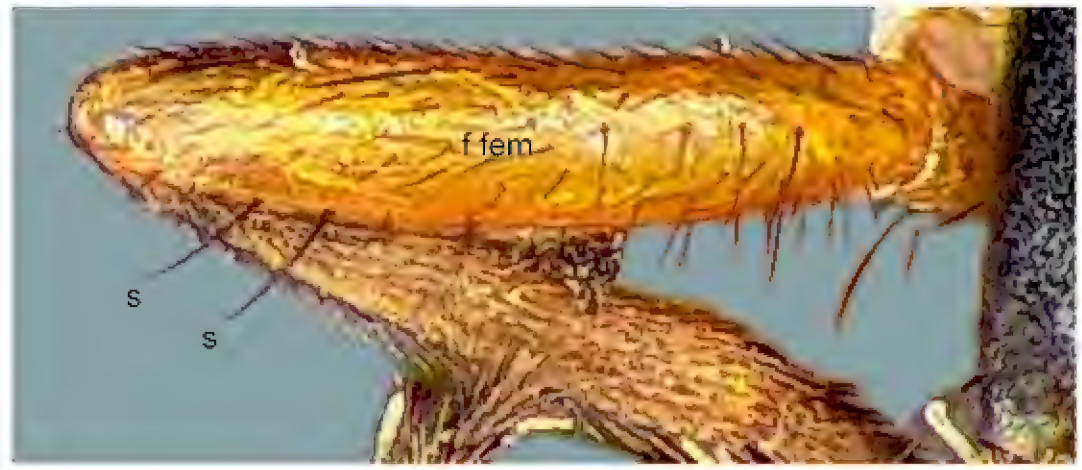


148 *Icteracantha* ♂

149 *Elassogaster* ♂



150 *Plagiostenopterina* ♂



151 *Pseudepicausta* ♂

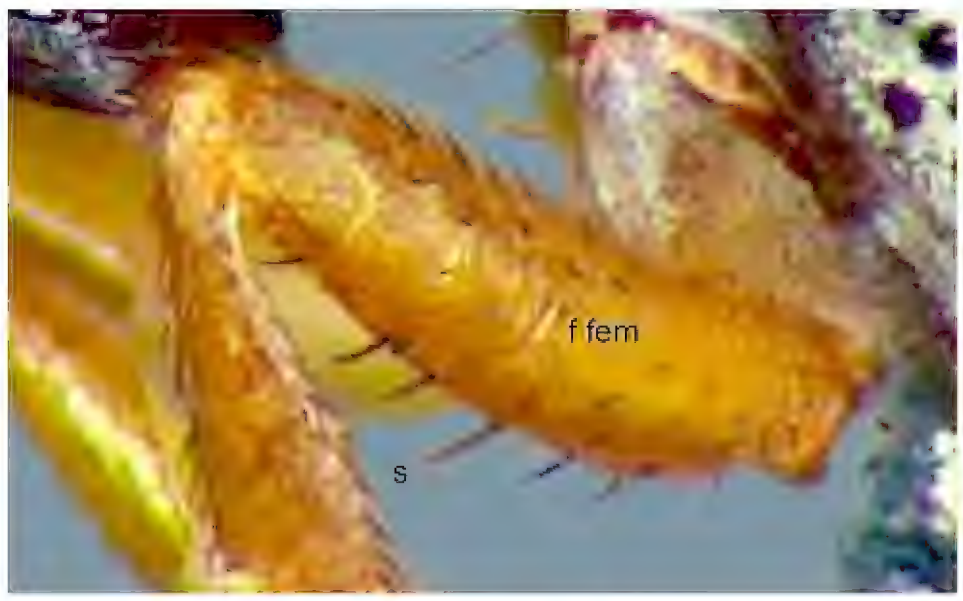
Figs 70.145–151. Femora of Platystomatidae: (145) fore femur of *Agrochira corniculata* Whittington, oblique anteroventral view ♂; (146) same, *Mesanopin tridens* Whittington, posterior view ♀; (147) same, *Icteracantha femorata* (Macquart) ♂; (148) mid femur of *I. femorata*, oblique posteroventral view ♂; (149) fore femur of *Elassogaster* sp., anteroventral and posteroventral views ♂; (150) same, *Plagiostenopterina* sp., posterior view ♂; (151) same, *Pseudepicausta* sp. ♂.

Abbreviations: f fem – fore femur; m fem – mid femur; s – seta; sp – spine; tub – tubercle.

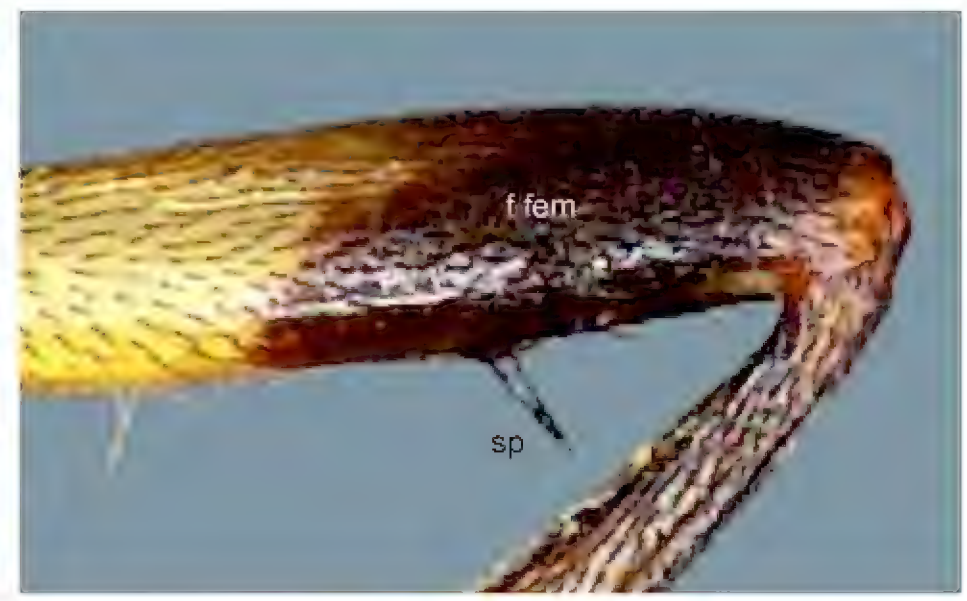
Scholastes, but are easily distinguished by the short, non-seriate branches on the antennal arista, two pairs of orbital setae and wing vein R_{2+3} straight or virtually so (Fig. 121). The frons only weakly narrows toward the vertex (in frontal view), is parallel-sided (Fig. 71), or widens toward the vertex (distinguishing the genus from *Parardelio*). In keeping with the subfamily characteristics, a katepisternal seta is inserted at the posterodorsal margin. Biology and immature stages remain unknown. Revision of the genus is needed and there is currently no identification key available.

Peltacanthina **Enderlein** (Platystomatinae)**.** An endemic genus of 53 described species, divided into two subgenera: *P.* (*Engistoneuroides*), with 11 species and *Peltacanthina sensu stricto*, with 42 species; widespread throughout the Afrotropical Region. Numerous undescribed species were noted in preparation of this chapter. The scutellar setae are inserted into tubercles rather than sessile (Fig. 86), distinguishing the genus; the two subgenera are separable on wing characters. *Peltacanthina* (*Engistoneuroides*) species possess only a few white crossbands in the apical half of the wing and no network of white maculae, whereas *Peltacanthina sensu stricto* species (Fig. 44), have numerous hyaline maculae (Fig. 122), or the wing membrane is uniformly brown. Occasional comments on specimen labels indicate that representatives of the genus oviposit in fallen fruit and dung. Biology and immature stages otherwise remain unknown. Revision of the genus is needed and there is currently no identification key available.

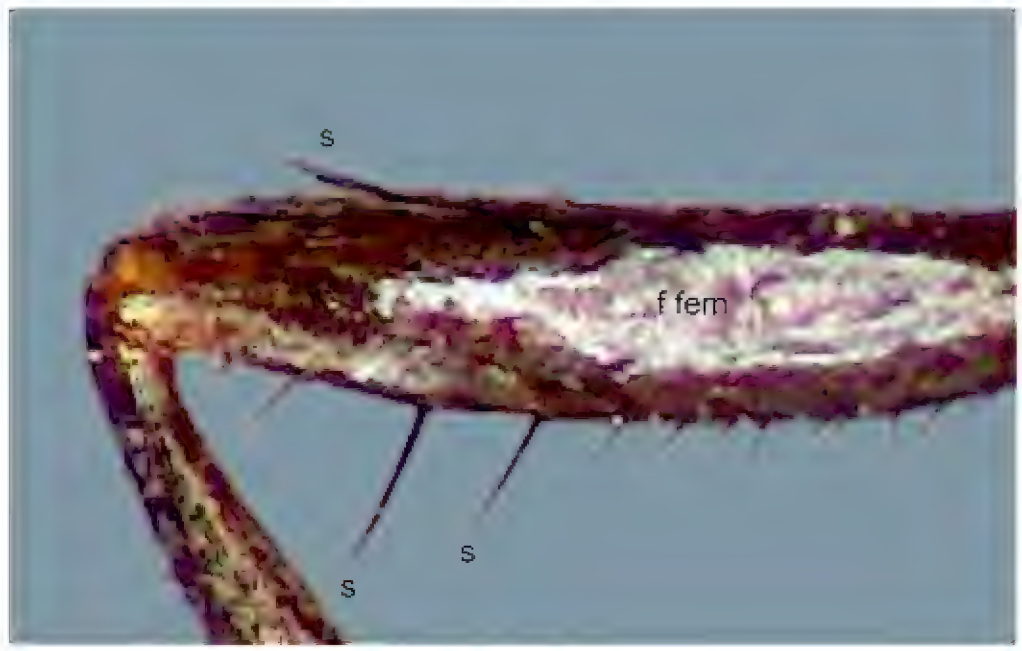
Phlebophis **Frey** (Platystomatinae)**.** An endemic monotypic genus, with the single described species, *P. serpentina* Frey, 1932, from Ghana and Nigeria. Few specimens are known for this highly distinctive species (Fig. 45), in which the inner and outer vertical setae of the head are unusually long; in addition, the strongly sinuous wing vein R_{2+3} and crossvein *dm–m* arched into cell *dm* (Fig. 123) are distinctive. *Phlebophis* was placed in the Platystomatinae by Steyskal (1980: 571), but without examining the male and dissecting the terminalia, so this placement cannot be confirmed. The lower calypter is reduced to a linear fringe and the subcostal wing vein (*Sc*) is angled sharply forward toward the costal vein (*C*) at the apex, suggesting the genus may belong to the Plastotephritinae. The subcostal vein (*Sc*) is not evanescent, however, as is the case in most Plastotephritinae. The presence of a katepisternal setula



152 *Lambia* ♂



153 *Phytalmodes* ♀



154 *Rivellia* ♀

155 *Scholastes* ♀

Figs 70.152–155. Fore femora of Platystomatidae: (152) *Lambia coelocephala* Hendel, oblique posterior view ♂; (153) *Phytalmodes africanus* Bezzi, anterior view ♀; (154) *Rivellia* sp., posterior view ♀; (155) same, *Scholastes vicarius* Hendel ♀.

Abbreviations: f fem – fore femur; s – seta; sp – spine.

would, however, place the genus in Scholastinae or Traphera-inae. In the absence of male terminalia characters, the genus is provisionally retained in Platystomatinae. Biology and immature stages remain unknown.

***Phytalmodes* Bezzi** (Platystomatinae)**.** An endemic genus of two Central African species: *P. africanus* Bezzi, 1908, described from Democratic Republic of Congo (Fig. 46); and *P. honestus* (Enderlein, 1924), described from Cameroon. No additional undescribed species are known. The apex of wing vein M_1 beyond crossvein *dm–m* and apex of vein R_{4+5} trace a parallel distinctive arc, before ending either side of the wing tip (Fig. 124). The wing membrane is brown at the base, with brown chevron-like cross bars at the wing apex, forming an inverted V-shape. The male gena is frequently elaborated by cone-shaped extensions (Fig. 72) and the fore femur often has a distinct sub-apical ventral spine (Fig. 153), but the extent of these characters appears to be variable and may not be useful as a diagnostic tool. Biology and immature stages remain unknown. Revision of the genus is needed and there are currently no comprehensive identification keys available.

***Piara* Loew** (Trapherinae)**.** An endemic monotypic genus, with the single described species, *P. cyanea* Hendel, 1914, described from "Afrika"; no other contemporary location data are available and no additional undescribed species are known. It is a distinctive genus, with the pterostigma very narrow (virtually absent), the subcostal vein (*Sc*) and vein R_1 meet the costal vein (C) very closely approximated and crossvein *r–m* is distal to the middle of cell *dm* and is slightly angled. Besides the condition of the narrow subcostal cell, specimens share a great similarity with specimens of *Traphera*. Biology and immature stages remain unknown.

***Plagiostenopterina* Hendel** (Platystomatinae)**.** A large genus of 33 described species occurring in the Afrotropical, Australasian and Oriental Regions (Fig. 47). Ten species occur in the Afrotropics, distributed in Central, Southern and West Africa, Madagascar and Seychelles. Several undescribed species from the region were noted in preparation of the above identification key. Malloch (1931) divided the genus into five subgenera, confusingly including *Elassogaster* as one of these, although this is still generally accepted as a valid genus and leaving most species unplaced. His partial treatment of species in the identification keys remains a problem. Species of *Plagiostenopterina* superficially resemble, and may be confused with, species of *Elassogaster* and *Pseudepicausta*. While many characters are shared between the three genera, such as general body form, head shape and setation and length of the antennal postpedicel, *Plagiostenopterina* is distinct in having microtrichia on the face (Fig. 73), setulae on the scutellum, widely distributed over the surface and not restricted to the lateral margin (Fig. 88); lateral postocular seta sometimes present (Fig. 74) and the male antennal arista sometimes with an apical palette (Fig. 75, arrow). In some species, wing cell *br* is brown in colour (Fig. 125) and this has previously been a character used to separate the genus from *Elassogaster* (McAlpine 2001), although it does not appear to hold true for all specimens. Little is known regarding the biology of the genus, but Whittington (2009: 314) reported specimens collected at elevations ranging from marine shorelines to *ca* 450 m, as well as specimens collected in bait traps in Seychelles. Revision of the genus is needed and there is currently no identification key available.

***Plastotephritis* Enderlein** (Plastotephritinae)**.** An endemic genus of five described species distributed on Central and West Africa. An additional two undescribed species are known from Democratic Republic of Congo. Generic affinities are clearly in the *Conopariella*-group, possibly close to *Pterogenomyia* or *Xyrogena*. These are medium-sized flies, body length: < 6 mm (4.7–5.7 mm), with yellow and brown bodies and distinctively dark brown and orange fasciate wings (Fig. 126), marked (particularly, but not exclusively) along the margins by hyaline markings (Fig. 48). In some cases, the brown maculae on the wing membrane are bullate. The head is compressed in both sexes. The female ovipositor is usually as long as the body length; the aculeus is 1.0–1.7 mm long, usually flattened in cross-section, bearing flat, apically acute cerci with moderately short lateral setulae, suggesting eggs are laid between tightly appressed plant axils. Species occur mainly in secondary Guinean rainforest and sometimes in agricultural lands. Plant associations are mostly unrecorded, but *P. patagiata* has been collected from *Macaranga hirifolia* Thou. (Euphorbiaceae). The biology and immature stages otherwise remain unknown. An identification key to the five species was provided by Whittington (2003).

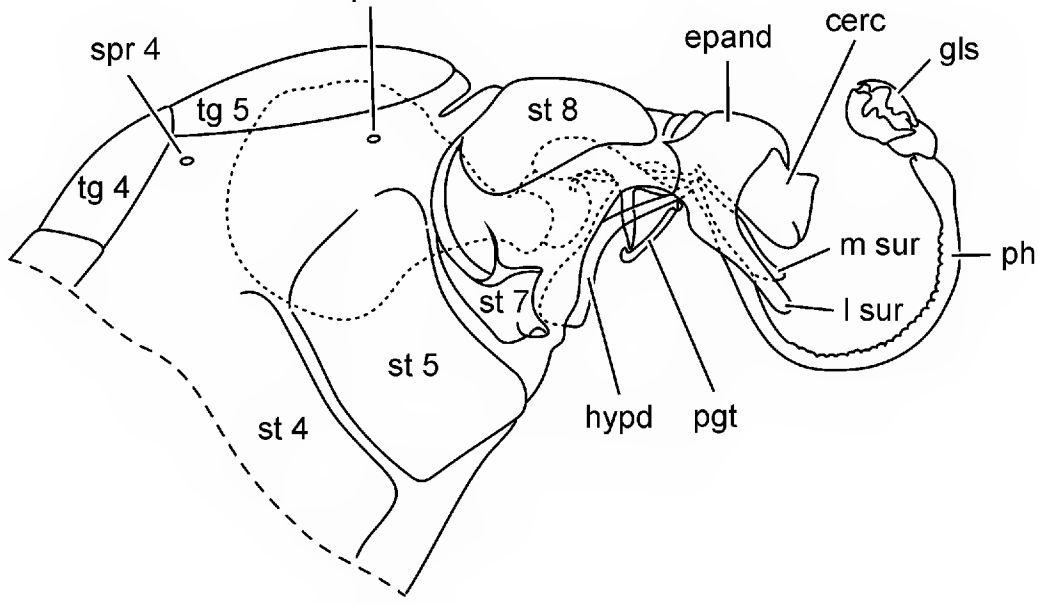
[***Polystodes* Robineau-Desvoidy** (Platystomatinae)**.** An endemic genus of two described species: *P. ichneumoneus* Robineau-Desvoidy, 1830, described from Senegal; and *P. metadacus* Speiser, 1915, from Cameroon. No additional undescribed species are known. The genus is similar to the genera *Elassogaster* and *Plagiostenopterina*, but can probably be separated by the single pair of apically inserted scutellar marginal setae (Speiser 1915), compared to both lateral and apical pairs in the other two genera. The name-bearing types of the two species have been lost and as no further material of the genus is available for study the genus is omitted from the above identification key. Biology and immature stages remain unknown. No key to the two species is currently available.]

***Prosopoconus* Enderlein** (Plastotephritinae)**.** An endemic monotypic genus, with the single described species, *P. fuscigenu* Enderlein, 1922, described from Equatorial Guinea and known only from the unique holotype. No additional undescribed species are known. This small-sized species (body length: < 4 mm) is easily distinguished by the protruding lower facial margin (Whittington 2003, fig. 528), which extends forward well-beyond the antennae. The body colour is buff, with dark brown markings and the wing membrane is brown with hyaline incisions in the basal third only (Fig. 127). Biology and immature stages remain unknown.

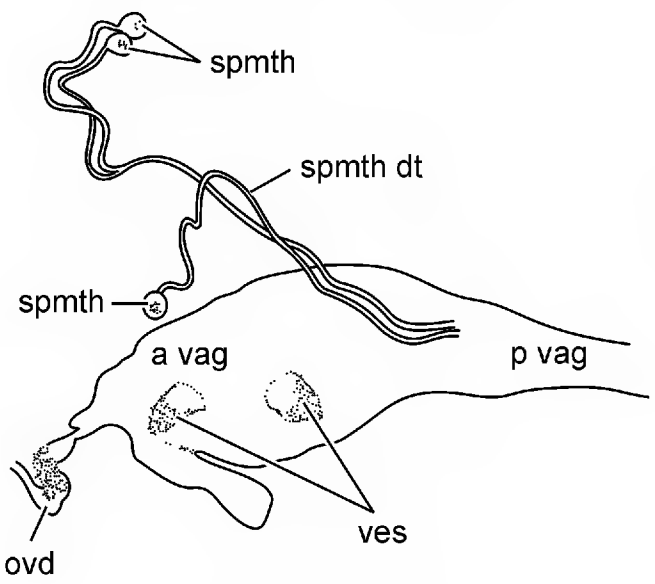
***Pseudepicausta* Hendel** (Platystomatinae)**.** A genus of 19 described species occurring in the Afrotropical, Australasian and Oriental Regions (Fig. 49). Four species occur in the Afrotropics, belonging to two subgenera: *P.* (*Parepicausta* Enderlein) and *Pseudepicausta sensu stricto*, both with two species each; known from Ethiopia, Mozambique, Tanzania, Togo and Zimbabwe. The presence of only one pair of apical scutellar setae distinguishes *P.* (*Parepicausta*) from *Pseudepicausta sensu stricto*, which has apical and marginal scutellar setae. Additional undescribed species are known from Cameroon, Côte d'Ivoire, Kenya, Madagascar, Nigeria and South Africa. The orbital setae are weakly developed, and in some species, only the posterior orbital seta is distinct from the setation of the frons (Fig. 79). A single lateral postocular seta is present (not clearly visible in Fig. 79, but see Fig. 74, for example). This is another

indication of the need to conduct cross-regional revisions for many genera assigned to Platystomatidae. *Pseudepicausta* superficially resemble, and may be confused with, species of *Elassogaster* and *Plagiostenopterina*. While many characters are shared between the three genera, such as general body form, head shape, setation and length of the antennal postpedicel (Fig. 79), *Pseudepicausta* is distinct in having wing cell r_{4+5} not narrowed toward the wing apex as veins R_{4+5} and M_1 are parallel and not bent prior to meeting the costal vein (C) (Fig. 128). The fore femur is ventrally setose (Fig. 151), without these being tuberculate as in *Elassogaster*. Biology and immature stages remain unknown. Revision of the genus is needed and there is currently no identification key available.

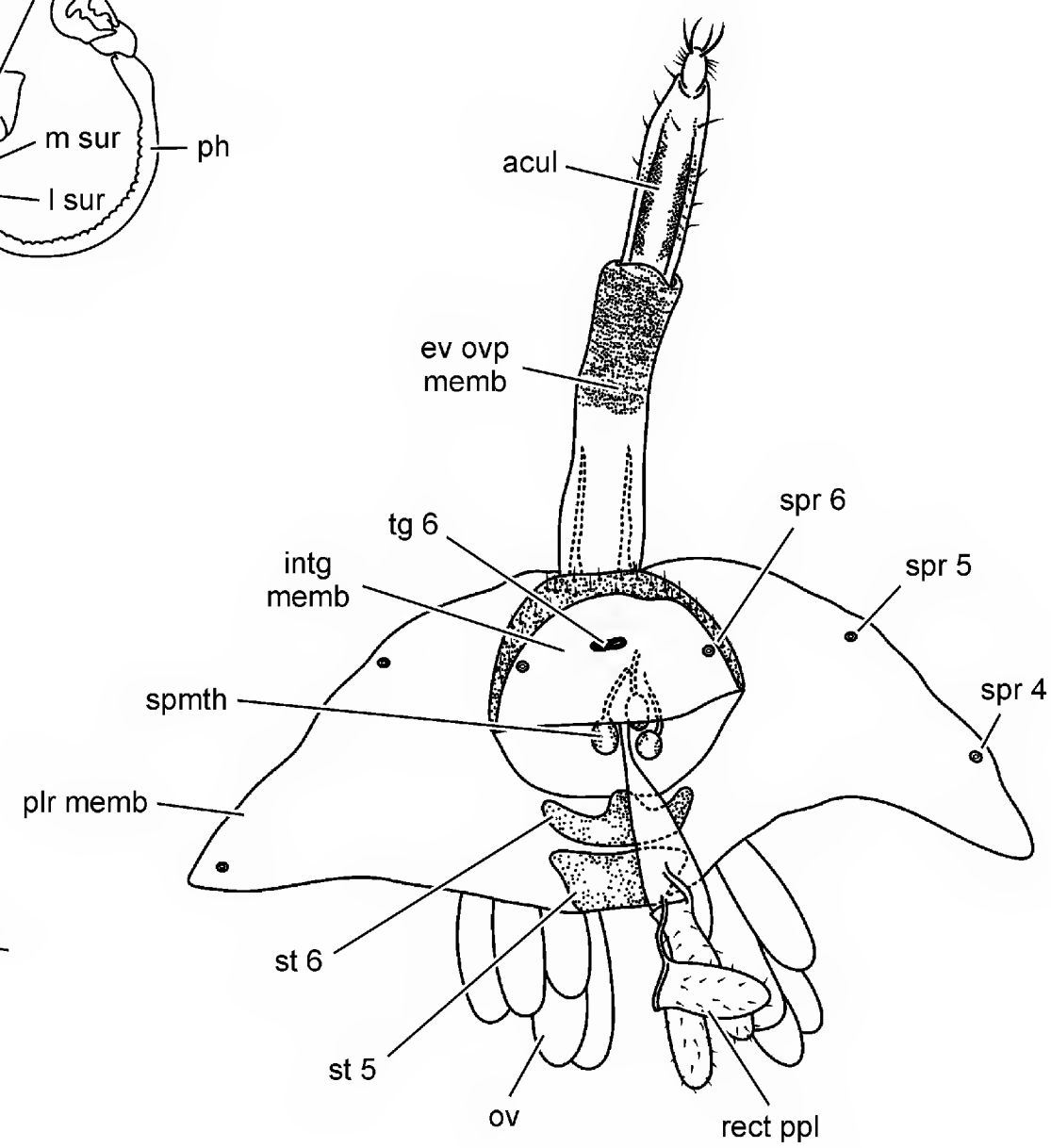
***Pseudoscholastes* Frey** (Scholastinae)**.** An endemic monotypic genus, with the single described species, *P. marshalli* Frey, 1932, recorded from Cameroon, Liberia and Sierra Leone. No additional undescribed species are known. In this species, the thorax is noticeably broad, equal to or broader than the entire length of the thorax and scutellum combined, giving the species a "dumpy" appearance (Fig. 50) and wing vein R_{4+5} is sinusoidal beyond crossvein *r–m* (Fig. 129). A distinct lateral postocular seta is present and the male arista is apically spatulate (Fig. 76). A specimen from Democratic Republic of Congo bears the label "Test cacao", which may refer to the cocoa tree, *Theobroma cacao* L. (Malvaceae). Biology and immature stages otherwise remain unknown.



156 *Pterogenomyia* ♂



158 *Pterogenomyia* ♀



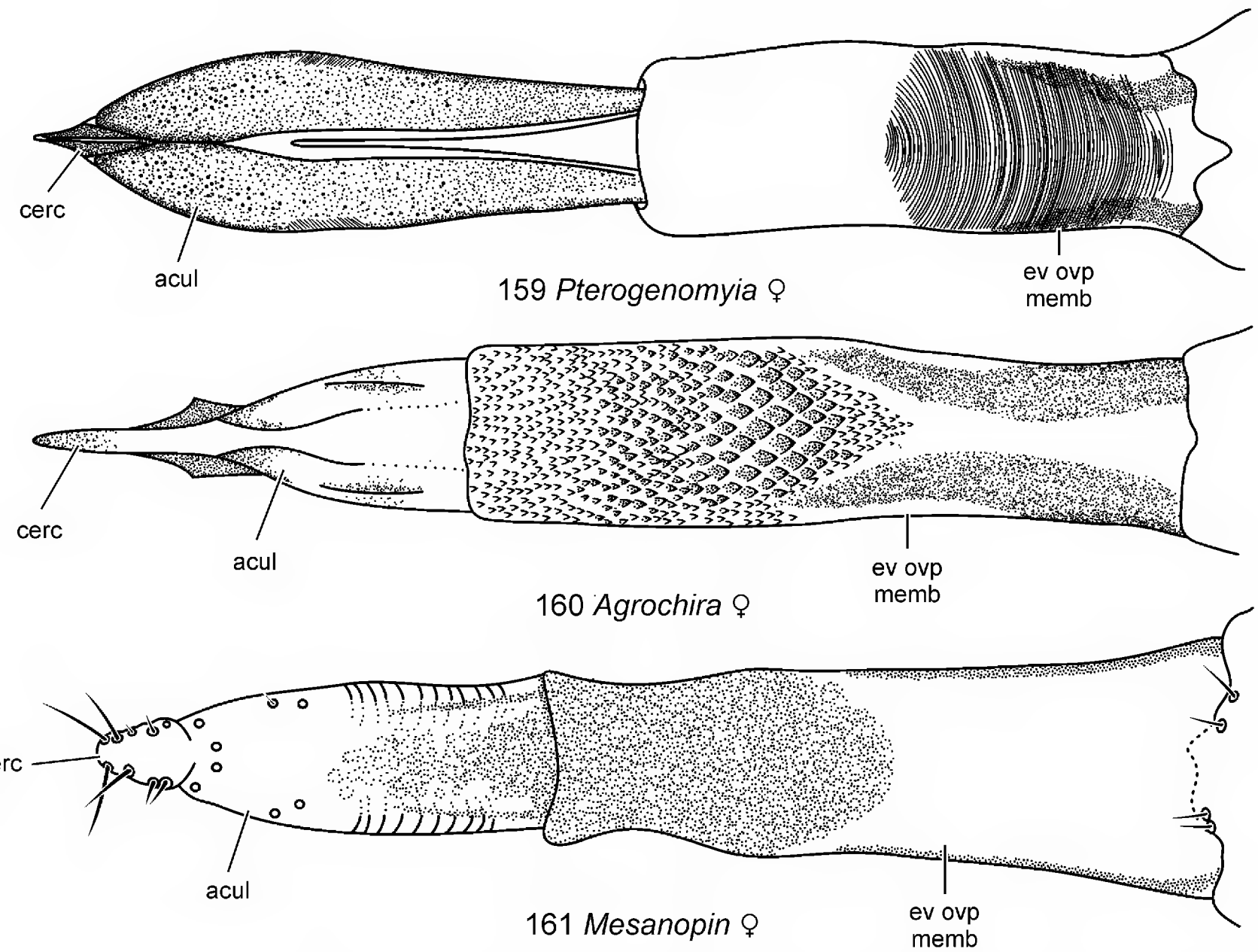
157 *Oeciotypa* ♀

Figs 70.156–158. Male and female terminalia of Platystomatidae: (156) male abdomen and terminalia of *Pterogenomyia picta* (Bigot), ventrolateral view; (157) female terminalia of *Oeciotypa rotundiventris* Frey, ventral view; (158) female internal organs of *P. picta*, lateral view. Figs 156–158 (after Whittington 2003, figs 539, 20, 23, respectively).

Abbreviations: a vag – anterior vagina; acul – aculeus; cerc – cercus; epand – epandrium; ev ovp memb – eversible ovipositor membrane; gls – glans; hypd – hypandrium; intg memb – intertergite membrane; l sur – lateral surstylus; m sur – medial surstylus; ov – ovariole; ovd – oviduct; p vag – posterior vagina; pgt – postgonite; ph – phallus; plr memb – pleural membrane; rect ppl – rectal papilla; spmth – spermatheca(e); spmth dt – spermathecal duct; spr – spiracle; st – sternite; tg – tergite; ves – vesicles.

***Pterogenomyia* Hendel** (Plastotephritinae)**.** Now regarded as an endemic monotypic genus, with the single species, *P. picta* (Bigot, 1891), recorded from Central and West Africa and Bioko Is. (Equatorial Guinea). Although up to five species names were previously applied (Steyskal 1980: 565 listed four), Whittington (2003) could find no convincing characters to separate these nominal species and a single name now applies. The name *P. picta* was not included in the checklist provided by Steyskal (1980: 565) and predated all that he included. The genus clearly belongs to the *Conopariella*-group, probably sharing affinities with *Conopariella* and *Federleyella* or *Plastotephritis*. Morphologically this is the largest species in the subfamily Plastotephritinae (Fig. 51), with a wing length reaching 12 mm. This distinctive species has a longitudinally orange, brown and hyaline fasciate wing membrane, without hyaline incisions along the margin (Fig. 130). The head is slightly compressed and the genae are extended and slightly bent forward, giving the head a triangular appearance in both sexes (in frontal view). The species occurs in climax and secondary rainforest and savanna woodland habitat types. The aculeus is rigid, flattened in cross-section, bearing flat, apically pointed, hard-tipped cerci with lateral setulae either short or absent. This shape suggests eggs may be deposited between tightly appressed plant axils or, less probably, by piercing live plant tissues (Fig. 159). Biology and immature stages otherwise remain unknown.

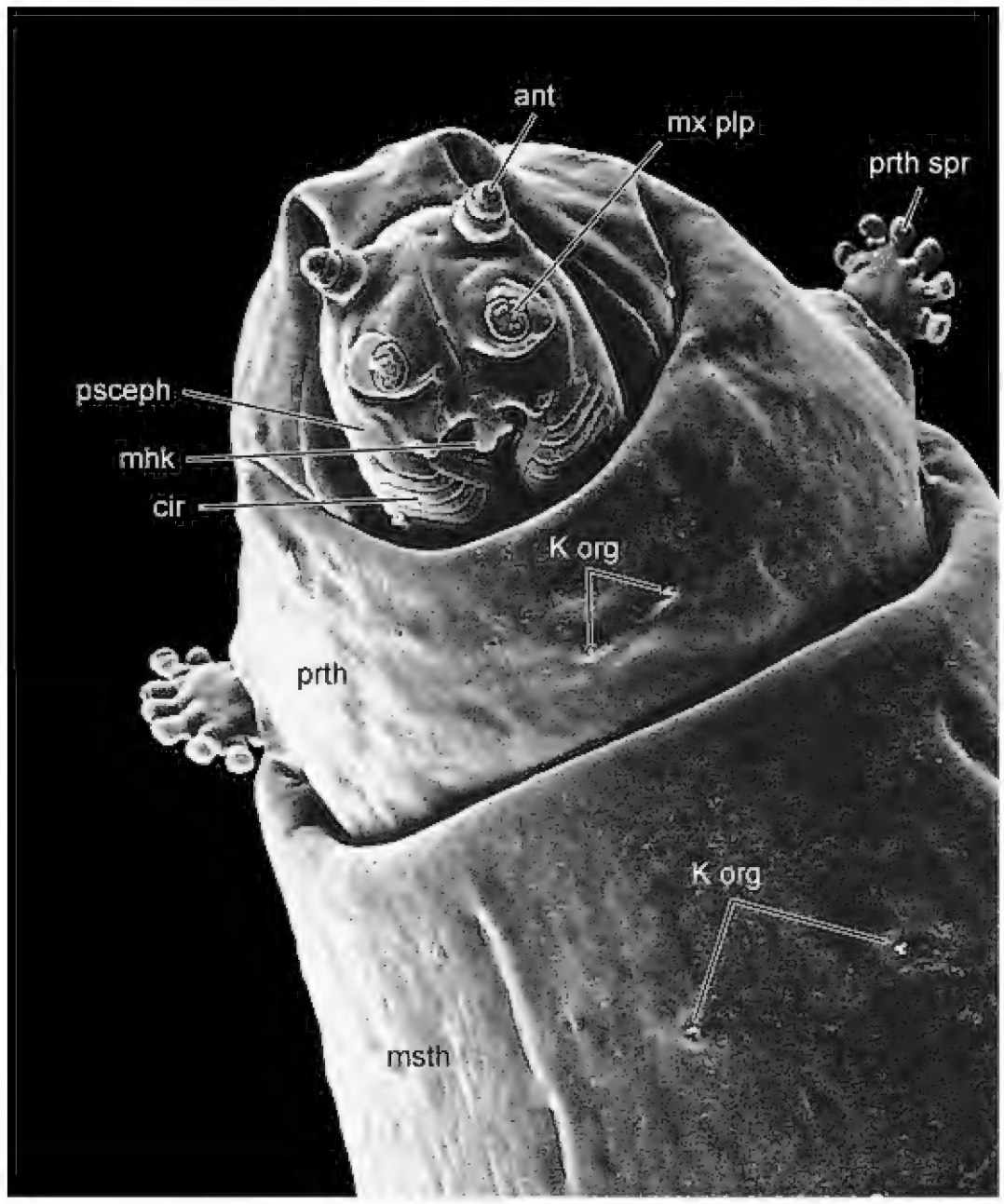
***Rivellia* Robineau-Desvoidy** (Platystomatinae)**.** A large, virtually cosmopolitan genus of 132 described species, occurring in all zoogeographical regions, except Antarctica. Twenty-six species occur in the Afrotropics, but the group requires revision and numerous additional undescribed species (and possibly a new closely related genus), are known from Cameroon, Democratic Republic of Congo, Madagascar, Togo and Uganda. In life, these flies often have an ant-like appearance and can be observed "strutting" on upper surfaces of leaves, waving the patterned wings in semaphore display (Whittington, pers. obs.). Morphologically similar to some Tephritidae, specimens of *Rivellia* (Figs 52, 131) could be overlooked in unsorted collections. Within the Platystomatidae, they resemble miniature specimens of *Elassogaster* (including sometimes having a lateral postocular seta present), but with a more compact antennal postpedicel and have affinities with *Neoardelio* and *Neoepidesma* (see above identification key for separation). The larvae of several species are known to have associations with nitrogen-fixing root nodules of leguminose plants and with roots of plants in other families (Whittington 2019). The only Afrotropical records are from Democratic Republic of the



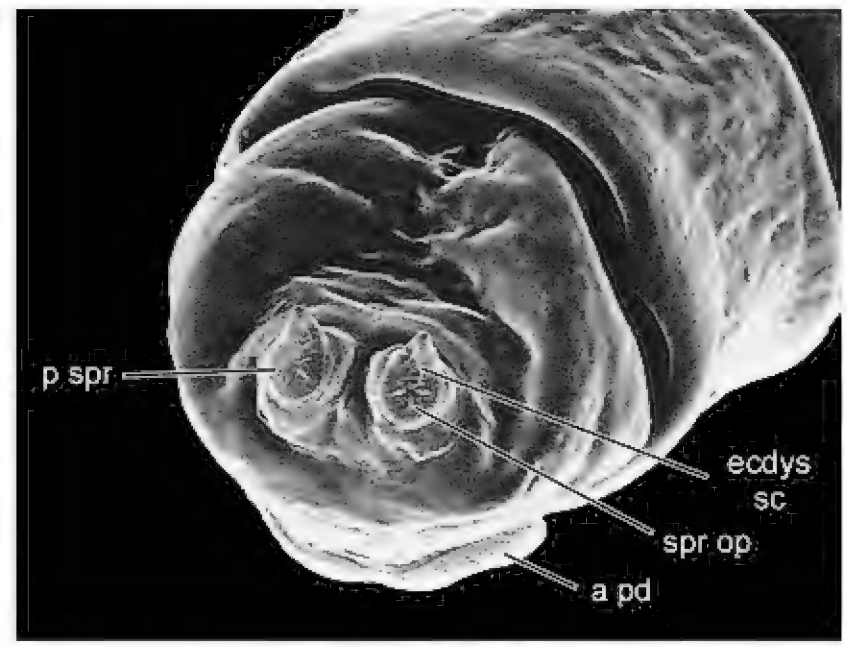
Figs 70.159–161. Female aculeus of Platystomatidae (ventral views): (159) *Pterogenomyia picta* (Bigot); (160) *Agrochira bicolor* Whittington; (161) *Mesanopin minax* Whittington. Figs 159–161 (after Whittington 2003, figs 536, 39, 401, respectively).

Abbreviations: acul – aculeus; cerc – cercus; ev ovp memb – eversible ovipositor membrane.

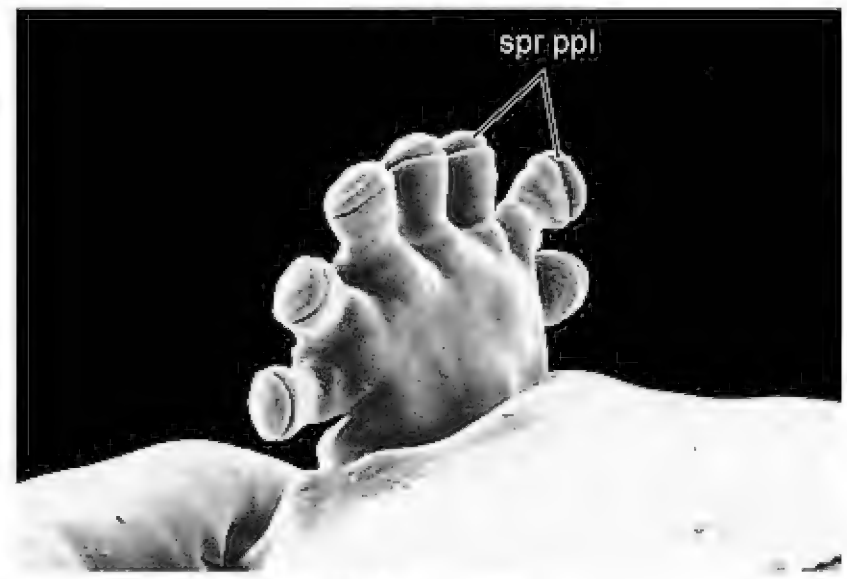
Congo (Seeger & Maldague 1960), where associations with root nodules of Groundnut, Soya and Mung bean, Cowpea and Bambara groundnut, *Voandzeia subterranea* (L.) Verdc. (all Fabaceae) were found and from Malawi, where Frey (1932) recorded *R. granulata* and *R. trimucronata* at an elevation of 1,000 m on Maize. Identification is hampered by a lack of identification keys and the group is in need of a global revision, to take the virtually cosmopolitan species into account.



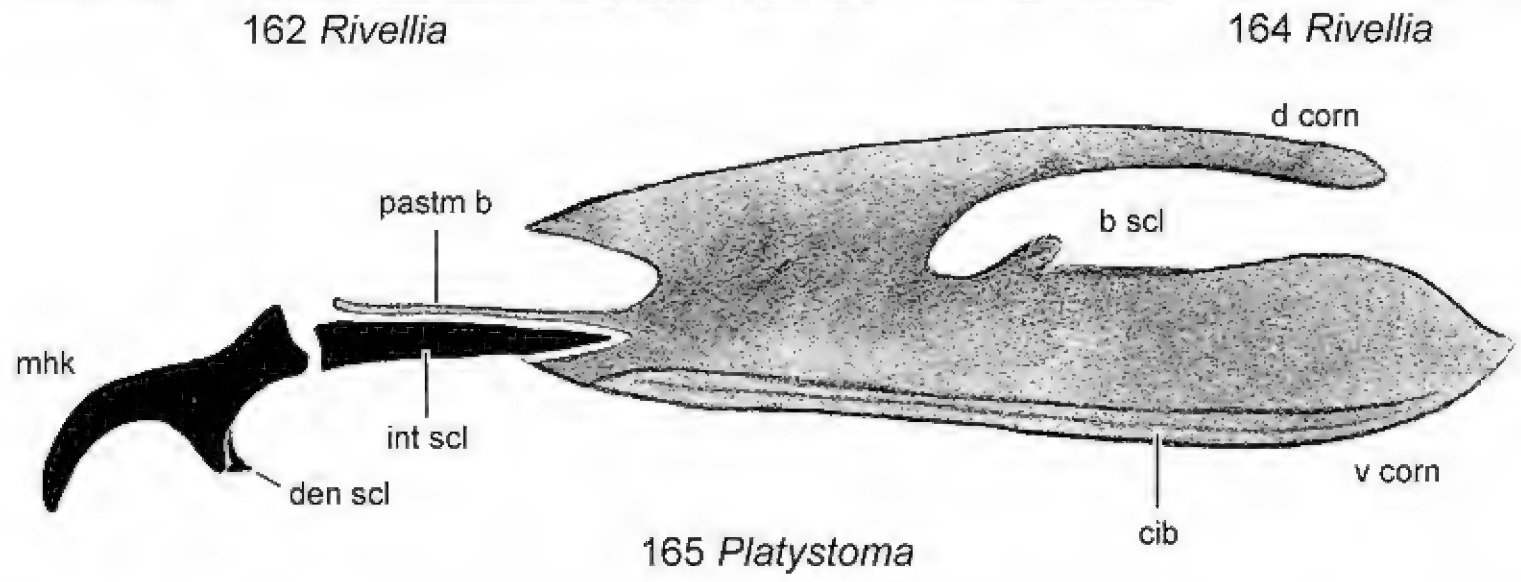
162 *Rivellia*



163 *Rivellia*



164 *Rivellia*



165 *Platystoma*

Figs 70.162–165. Immature stages of Platystomatidae: (162) electron micrograph of pseudocephalon and thorax of *Rivellia pallida* Loew, ventral view (non-Afrotropical); (163) same, posterior view of caudal segment; (164) same, prothoracic spiracle, lateral view; (165) cephaloskeleton of *Platystoma euphorbium* Enderlein (non-Afrotropical). Figs 162–164 (after Bibro & Foote 1986, figs 3, 6, 4, respectively), Fig. 165 (after Hennig 1945, fig. 5).

Abbreviations: a pd – anal pad; ant – antenna; b scl – basal sclerite; cib – cibarium; cir – cirri; d corn – dorsal cornu; den scl – dental sclerite; ecdys sc – ecdysial scar; int scl – intermediate sclerite; K org – Keilin's organs; mhk – mouthhook; msth – mesothorax; mx plp – maxillary palpus; p spr – posterior spiracle; pastm b – parastomal bar; prth – prothorax; prth spr – prothoracic spiracle; psceph – pseudocephalon; spr op – spiracular opening; spr ppl – spiracular papillae; v corn – ventral cornu.

***Scholastes* Loew** (Scholastinae)**.** A genus of 13 described species occurring in the tropical parts of the Afrotropical, Australasian and Oriental Regions. Only a single species, *S. vicarius* Hendel, 1912, is recorded from the Afrotropics, where it was thought to be restricted to Seychelles, although subsequently the species has been found to occur on all three Mascarene Islands (*i.e.*, Mauritius, Réunion Is. and Rodrigues Is.) (A.H. Kirk-Spriggs, pers. obs.). No additional undescribed species are known from the region. It is a distinctive genus (Fig. 53), with a raised transverse ridge on the lower frons above the ptilinal fissure (Fig. 68), pale transverse bands across the face and frons (Fig. 13) and a short plumose antennal arista. Besides these distinctions, the following characteristics separate *Scholastes* from similar looking, but smaller flies assigned to *Parardelio* and *Paryphodes*: arista with long bipectinate microtrichia; one orbital seta (Fig. 81); and wing vein R_{2+3} sinusoidal (Fig. 132). Specimens from Seychelles were observed visiting a ripe fallen banana (Whittington 2009: 316), potentially for oviposition, but the presence of males suggests that feeding and courtship may also be implicated; further specimens were taken from bait traps. Biology and immature stages are otherwise unknown.

***Seguyopiara* Steyskal** (Trapherinae)**.** An endemic genus of four described species: *S. apicalis* (Frey, 1932), described from South Africa; *S. azurea* (Hendel, 1914), from Uganda, *S. fasciata* Steyskal, 1990, described from Cameroon and Nigeria and *S. kaplanae* Steyskal, 1990, from Cameroon at *ca* 1,200 m. No additional undescribed species are known. Representatives of the genus are *ca* 4–5 mm in length and are distinct in having the following combination of characters: two pairs of marginal scutellar setae, wing cell *bm* normally shaped, crossvein *dm-m* perpendicular to vein M_1 (Fig. 133), arista with short nonseriate branches, face strongly convex (as in Fig. 82) and the head with two pairs of orbital setae (the last two named characters shared with *Parardelio*, *Paryphodes* and *Piara*). In general appearance (Fig. 54), representatives of the genus are shiny, metallic blue, with dark brown patterned wings, not unlike *Traphera*, which has six marginal scutellar setae. *Seguyopiara fasciata* reportedly occurs at elevations between 1,000 m and 1,800 m (Steyskal 1990). Biology and immature stages otherwise remain unknown. An identification key to the four species was provided by Steyskal (1990).

***Sphenoprosopa* Loew** (Platystomatinae)**.** An endemic monotypic genus, with the single described species, *S. fascipennis* (Macquart, 1846), recorded from Mozambique and South Africa. It is a highly distinctive genus (Fig. 55), with sloping frons and antennae ventral to the middle of the compound eye (Figs 55, 80). Due to the combination of wing crossveins *r–m* and *dm–m* closely approximated (distance between *r–m* and *dm–m* less than length of *dm–m*) (Fig. 134) and head and body white microtrichose with bare maculae surrounding setulae and setae resulting in a reticulate pattern, a close affinity is shared with the genus *Lambia*, from which *Sphenoprosopa* is distinguished by the positioning of the antennal insertion. No additional undescribed species are known. Biology and immature stages remain unknown.

***Stellapteryx* Whittington** (Plastotephritinae)**.** An endemic genus of two described species: *S. minuta* Whittington, 2003 and *S. stellata* Whittington, 2003, both of which are confined to forested parts of Madagascar. No additional undescribed species are known. These are small (body length: < 5 mm), predominantly pale yellowish white species, with brown markings, having a slight metallic blue lustre under certain lights. The brown wing membrane is mottled with hyaline maculae and incisions (Fig. 135). No sexual dimorphism is apparent in the head, but males bear a modified "scoop" on the dorsal surface of the hind trochanter and distally on the hind tibia, which may serve pheromone release functions (White 1999: 508). The genus is probably associated with other genera in the *Cladoderris*-group, but with no clear affinities based on external morphological characters. Biology and immature stages remain unknown. An identification key to the two species was provided by Whittington (2003).

***Traphera* Loew** (Trapherinae)**.** An endemic monotypic genus, with the single species, *T. chalybea* (Wiedemann, 1840), described from South Africa. No additional undescribed species are known. Steyskal (1980: 574) listed three species in the genus, but later (Steyskal 1990), transferred two of these to the newly described genus *Seguyopiara*, representatives of which are distinctive in having four marginal scutellar setae, compared to six marginal scutellar setae in *T. chalybea*; the latter species is dark brown, with distinctively slanted fasciae on the wing membrane (Fig. 136). The body is metallic, contrasting with the orange head (Figs 56, 82); there are six scutellar marginal setae and wing crossvein *bm–m* is half as long as, or shorter than vein *Cu* and crossvein *dm–m* is at an acute angle to vein M_1 (Figs 136, 144). Specimens of *Piara* also resemble representatives of *Traphera*, but have a very narrow subcostal cell (*sc*). Biology and immature stages remain unknown.

***Venacalva* Whittington** (Plastotephritinae)**.** An endemic genus of four described species: *V. dichas* Whittington, 2003, described from Democratic Republic of Congo; *V. margarita* Whittington, 2003, described from Ghana, Nigeria and Sierra Leone; *V. seriata* (Enderlein, 1924), recorded from Cameroon, Democratic Republic of Congo and Sierra Leone; and *V. virga* Whittington, 2003, described from Togo. No additional undescribed species are known. The general morphology suggests a close affinity to the genus *Atopocnema*. These are small-sized flies (body length: < 5 mm), that are predominantly pale yellowish white to pale brown, with fewer distinctive brown markings than other Plastotephritinae (Fig. 57). The wing membrane is brown, marked with scattered hyaline maculae (Fig. 137), the cercus of the female ovipositor is ovoid, apically blunt and bears moderately long ventral and dorsal setulae; the prosternum is bullate. The male hind trochanter is also sometimes strongly modified with lobes. Biology and immature stages remain unknown. An identification key to the four species was provided by Whittington (2003).

***Xyrogena* Whittington** (Plastotephritinae). An endemic genus of 12 described species, distributed in Central, East and West Africa. No additional undescribed species are known. The plumose antennal arista and sexual dimorphism of the male gena and hind leg suggests a close affinity with the *Conopariella*/*Federleyella* genus pair. Small- to medium-sized flies (body length: 3.3–5.9 mm). Generally yellow with brown markings (Fig. 58), the head distinctively compressed and the antennal arista noticeably plumose. The wing membrane is brown, sometimes with orange-yellow patches, intersected by hyaline incisions, maculae and sometimes fasciae (Fig. 138). They are sexually dimorphic, with the male gena laterally expanded, giving the head a triangular shape in frontal view,

the male hind trochanter is moderately modified and the hind tibia is distally expanded, presumably for pheromone transfer (White 1999: 508). The female ovipositor has the cercus ovoid and apically blunt, bearing moderately long ventral and dorsal setulae, suggesting that eggs are deposited within cracks or crevices in the substrate. The genus has been sampled in climax, Guinean riparian and swamp forest types. Biology and immature stages otherwise remain unknown. An identification key to the 12 species was provided by Whittington (2003).

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TEPHRITIDAE 71

(True Fruit Flies)

David L. Hancock, Amnon Freidberg† and Ariel-Leib-Leonid Friedman

Fig. 71.1. Female of *Dacus* (*Didacus*) *vertebratus* Bezzi (Namibia) (photograph © S.A. Marshall).

Diagnosis

Small- to large-sized (body length: 2.0–21.0 mm; excluding female ovipositor) acalyptrate flies, often superficially resembling wasps or spiders, usually with patterned wings (Figs 1, 2); defining character of the family being 3 costal breaks in the wing, proximal and distal to humeral vein (*h*), immediately basal to end of subcostal wing vein (*Sc*), which ends before costal vein (C) in all subfamilies, except Tachiniscinae; frontal setae almost invariably present even if small; body variously coloured, metallic in some Malagasy taxa (e.g., *Meracanthomyia* Hendel (Adramini) and *Trirhithrum* Bezzi (Ceratitidini)).

Head (Figs 3, 4, 6–15) with 3 ocelli, except in *Bibundia* Bischof (Tachiniscinae); frons with 2–4 inclinate frontal setae (Figs 6–12) (more in some extralimital taxa), sometimes reduced or absent in wasp-mimics (e.g., *Dacus* F. and some Adramini) and 1 or 2 orbital setae (Figs 6–11) (rarely 3 in some extralimilal taxa), at least anterior pair reclinate or, in males of some *Ceratitis* MacLeay *sensu stricto* species, with anterior pair reclinate, expanded apically; row of postocular setae usually present (Figs 2, 6, 7, 10, 11), generally thin and black, but often thickened and yellow or white in subfamily Tephritinae (Figs 8, 9); ocellar and vertical setae usually well-developed (Figs 6–11); ocellar setae rudimentary or absent in Acanthonevrini and some Trypetinae; preocellar interfrontal setae occur in some Schistopterini genera and medial postocellar setae occur in some Tephritini genera.

Thorax (Fig. 5) with anepisternum with vertical phragma (externally manifested as suture) in posterior ⅓ (often obscured in densely microtrichose species); anepimeron usually with at least 1 seta medially. Scutellum (Fig. 5) usually with 1–3 pairs of marginal setae (more in some Tachiniscinae), basal pair absent in most Afrotropical Dacini, apical pair reduced or absent in many Tephritinae and medial pair present only in some Blepharoneurinae and Acanthonevrini. Wing (Figs 16–173) hyaline, variously patterned or entirely dark, sometimes with silvery maculae ("argents") or dark, raised and rounded swellings ("bullae"); distinct costal setae often present at basal margin of

third costagial break; subcostal vein (*Sc*) anteriorly turned, evanescent after turn, ending before costal vein (*C*) in all subfamilies, except in some Tachiniscinae (Fig. 16); vein R_1 densely setulose dorsally to base, this row of setulae often interrupted posterior to apex of vein *Sc* in many Tephritinae, leaving bare gap; basal medial cell (*bm*) expanded, subrectangular in Dacini, otherwise narrow or subtriangular; anterior cubital cell (*cua*) often with short or elongate apical extension.

Abdomen of variable shape, from broadly oval to narrowly elongate; sternites 1 and 2 not fused; all tergites fused in *Dacus*; male (Figs 177–179) with long, coiled phallus, stored between postabdomen and tergite 5 at rest, bearing stout apical glans (Fig. 180); lateral surstylus fused to epandrium (Fig. 179); medial surstylus closely associated with lateral surstylus, bearing 2 (rarely 0–1) pairs of prensisetae; female (Figs 181, 182), usually with ovipositor of piercing type, including strongly sclerotised, pointed or serrated aculeus (Fig. 183), telescoping into well-developed oviscape that opens posteroapically in all, except Tachiniscinae, in which case opens dorsoapically; aculeus needle-like or dorsoventrally or laterally compressed, sometimes less sclerotised with more or less rounded cercal unit bearing relatively long preapical setae ("tactile" type, especially in Acanthonevrini); 2 or 3 spermathecae present (rarely 4 in some extralimital taxa) (Fig. 182), often rounded or club-shaped, but long and coiled in many Dacinae; spermathecal ducts separated until just prior to genital chamber.

Egg 0.35–1.65 mm in length, white to pale brown, elongate-oval to pedunculate, often slightly curved and smooth to rugose textured, often with raised areas in hexagonal or similar shapes; micropyle apical to sub-apical and usually noticeable; some species with slender lobe, sometimes extremely elongate at anterior end; chorionic respiratory system well-developed, with aeropyles confined to anterior end; without plastron and hatching lines.

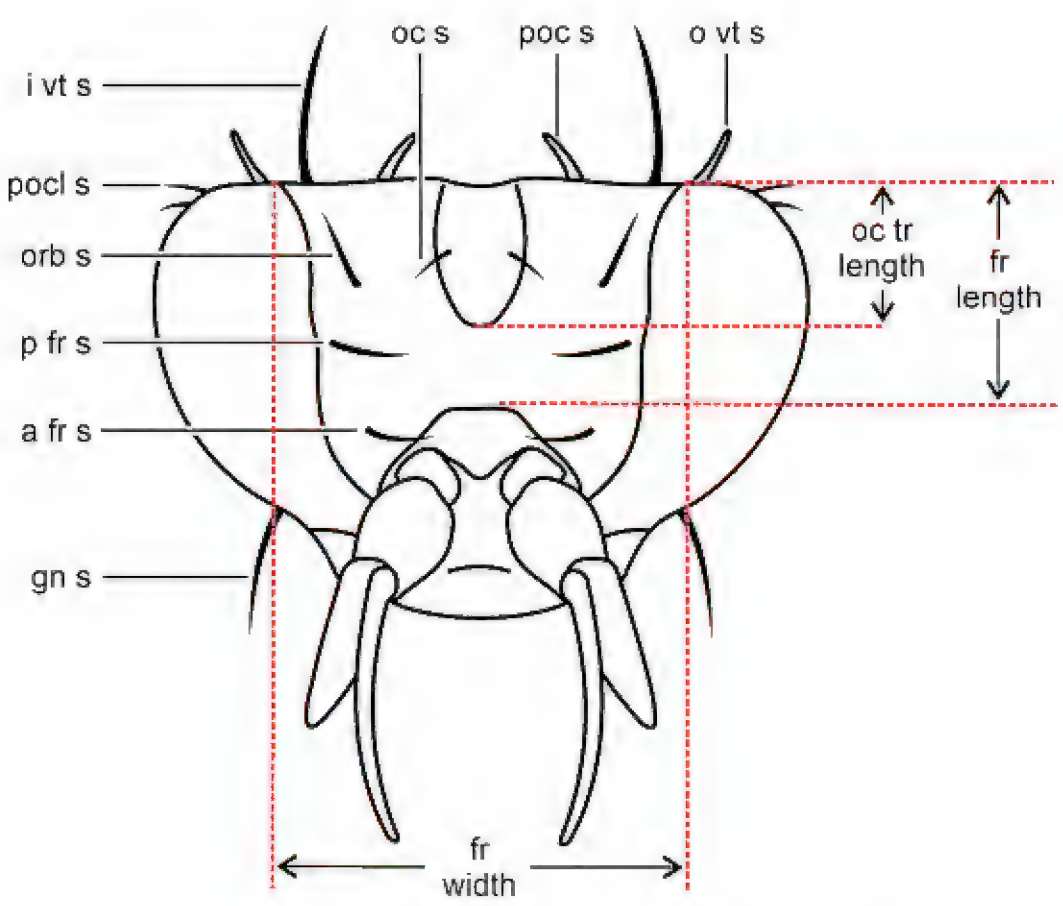
Larvae white to yellow, occasionally with darker caudal or ventral areas; in most species elongate, cylindrical, tapering anteriorly, but in gall- and flower-breeding taxa sometimes stout, subspherical; first-instar with metapneustic respiratory system, second- and third-instars amphipneustic; prothoracic spiracle (Fig. 185) sessile, or virtually so, usually fan-shaped or bimodal, with 2–53 papillae; cephaloskeleton (Fig. 184) typically muscomorphan, with right and left mouthhooks equally developed, with 1 or 2 sub-apical teeth in first- and second-instars, 0–2 in third-instar; posterior spiracular plate (Fig. 186) unpigmented, without peritreme, spiracular openings straight, in third-instars 3 openings oriented radially from ecdysial scar, subparallel to perpendicular to one another (in frugivorous species angle between dorsal and ventral openings usually no more than 90°, but angle greater in some Tephritinae).

Puparium (Fig. 188) usually barrel-shaped, rarely bean-shaped, or with flattened caudal segment, smooth or wrinkled, with distinct or indistinct segmentation; colour white to yellow, brown or black, colour may vary from anterior to posterior ends.

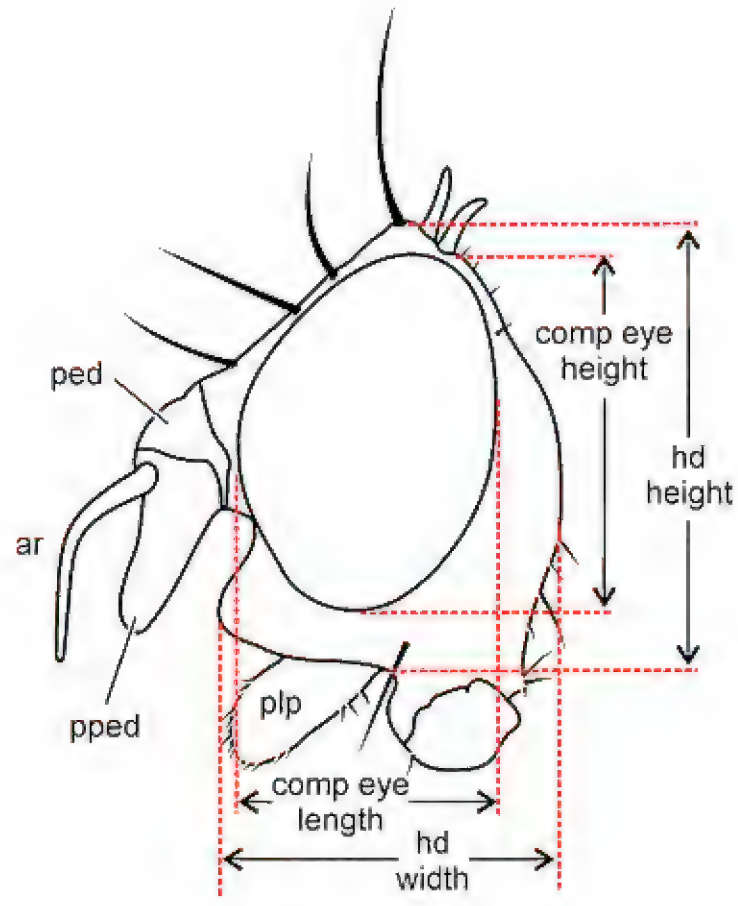
Adult Tephritidae are most commonly confused with other picture-winged flies in the Afrotropics, particularly the

Fig. 71.2. Living example of female *Ceratitis* (*Ceratalaspis*) *cosyra* (Walker) (Namibia) (photograph © S.A. Marshall).

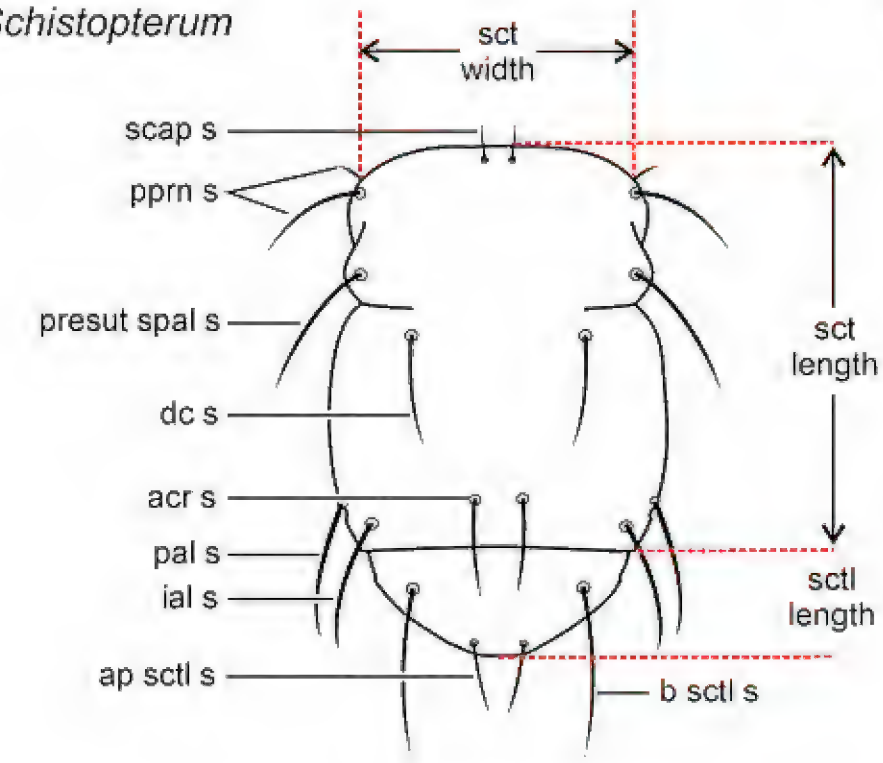
Platystomatidae (see Chapter 70). Many species have a distinct apical extension on the anterior cubital cell (*cua*), a character shared with the Pyrgotidae (see Chapter 72) and many Ulidiidae (see Chapter 69), but this extension is very weak or absent in some genera, particularly in Tephritinae; it is absent in all Platystomatidae. Three costal breaks, an abbreviated subcostal vein (except in some Tachiniscinae), usual presence of distinct frontal and orbital setae and lack of metallic body colouration (except in some Malagasy taxa) readily separate them. Most, if not all species in subfamily Dacinae appear to be mimics of wasps in the tribe Dacini and of jumping spiders (Salticidae) in the tribes Ceratitidini and Gastrozonini. Many species in the subfamily Trypetinae also appear to be wasp- or spider-mimics, particularly those that display openly on the upper surfaces of



3 *Schistopterum*



4 *Schistopterum*



5 *Schistopterum*

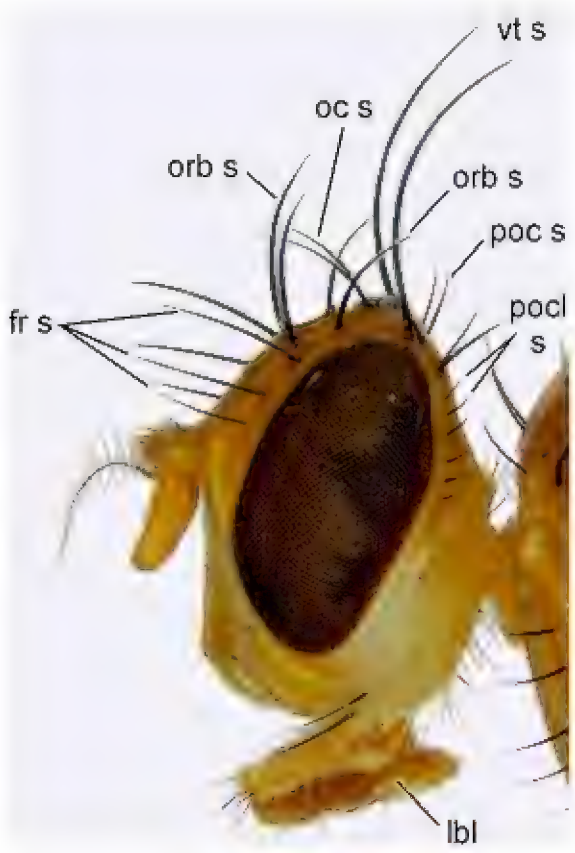
Figs 71.3–5. Diagrammtic representation of heads and thorax of Tephritidae (indicating setation): (3) head of *Schistopterum* sp., dorsal view; (4) same, lateral view; (5) same, thorax, dorsal view. Figs 3–5 (Gidron 2014, figs 1A–C).

Abbreviations: a fr s – anterior frontal seta; acr s – acrostichal seta; ap sctl s – apical scutellar seta; ar – arista; b sctl s – basal scutellar seta; comp eye – compound eye; dc s – dorsocentral seta; fr – frons; gn s – genal seta; hd – head; i vt s – inner vertical seta; ial s – intra-alar seta; o vt s – outer vertical seta; oc s – ocellar seta; oc tr – ocellar triangle; orb s – orbital seta; p fr s – posterior frontal seta; pal s – postalar seta; ped – pedicel; plp – palpus; poc s – postocellar seta; pocl s – postocular seta; pped – postpedicel; pprn s – postpronotal setae; presut spal s – presutural supra-alar seta; scap s – scapular seta; sct – scutum; sctl – scutellum.

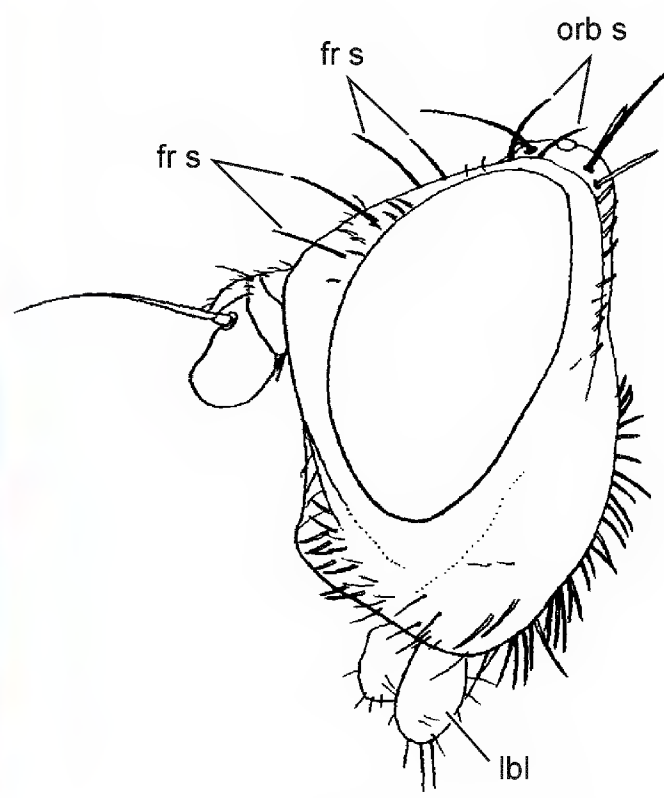
leaves. Acanthonevrini, which display on tree trunks or on the undersides of leaves, are more cryptically patterned.

Biology and immature stages

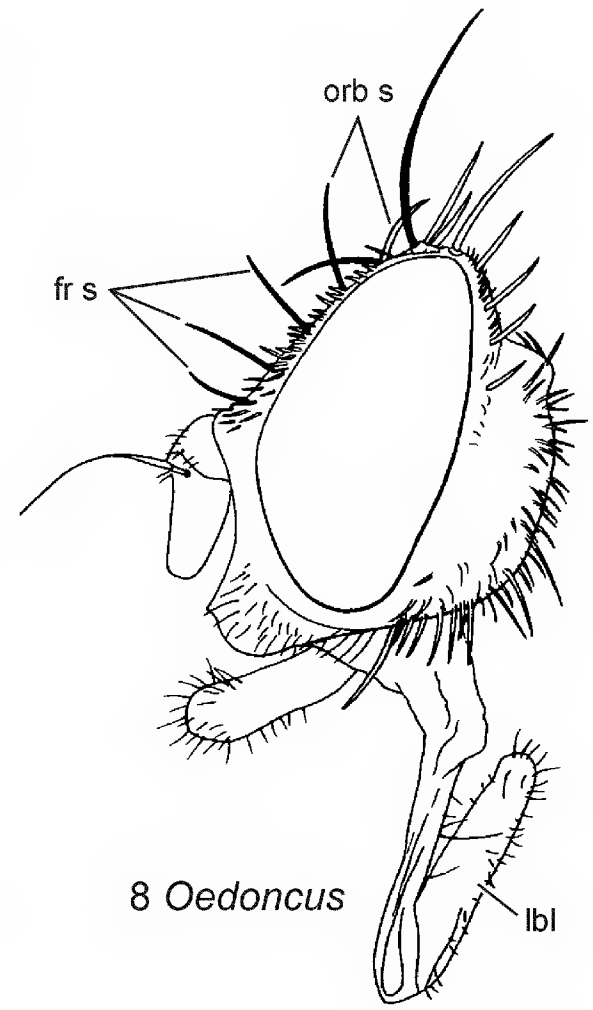
The earliest biological studies on Afrotropical Tephritidae were undertaken by Munro (1925, 1926, 1929, 1935) on the South African fauna. Most studies since then have focused on the discovery of host-plants, details of which are provided in the "Classification" and "Synopsis of the fauna" sections below. The tribe Tachiniscini are parasitic on Lepidoptera, Acanthonevrini are mostly saprophagous and other groups are phytophagous, utilising the fruit, stems, leaves or flowers of numerous botanical families. Notes on the immature stages of several Egyptian genera were provided by Efflatoun (1925, 1927) and



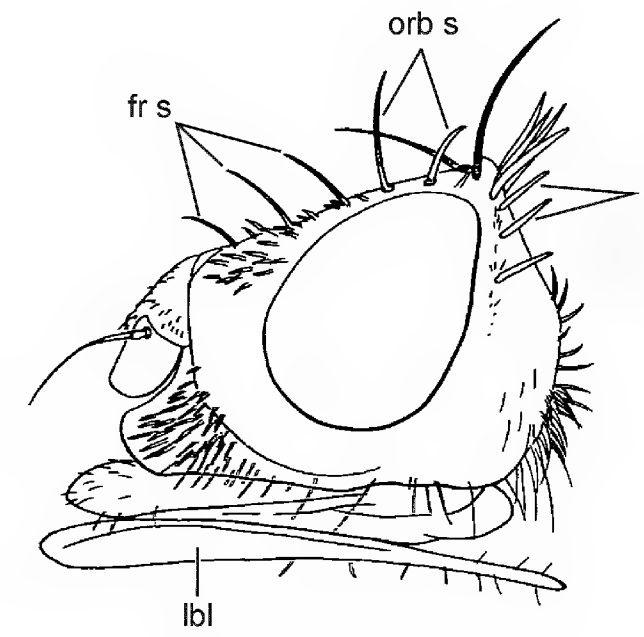
6 *Ceratitoides*



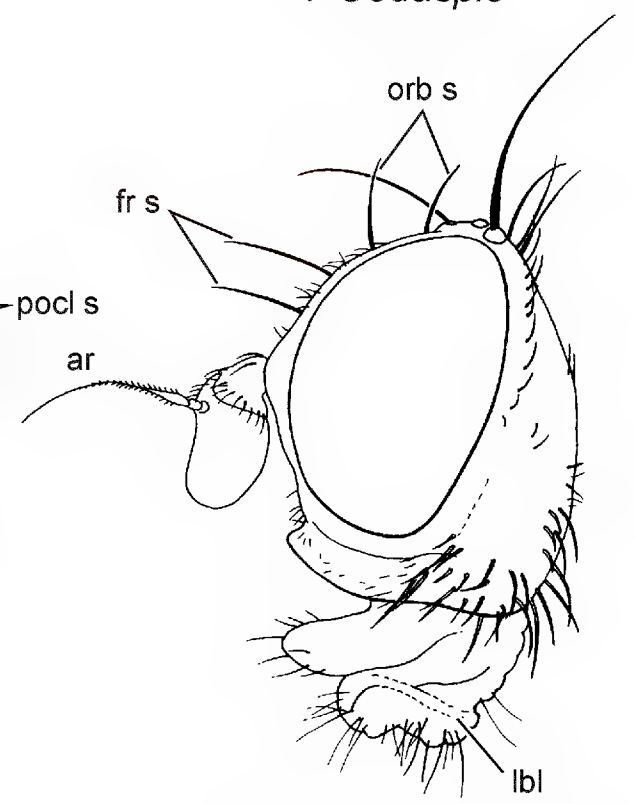
7 *Oedaspis*



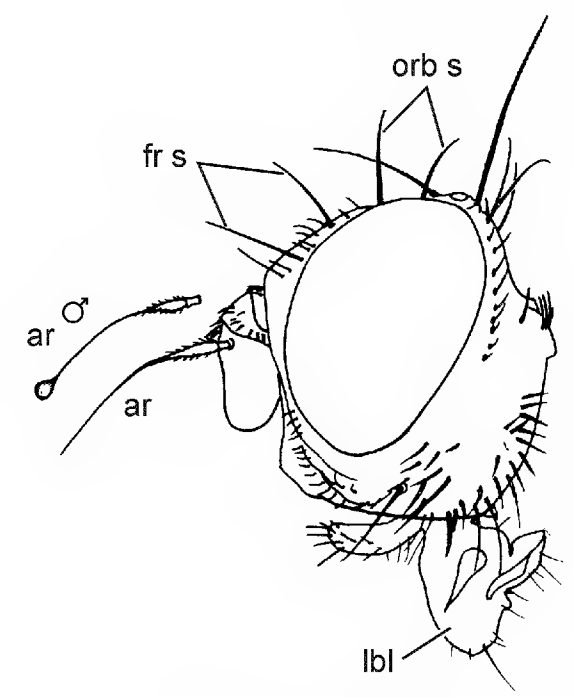
8 *Oedoncus*



9 *Xenodorella*



10 *Cryptophorellia*



11 *Orthocanthoides* ♀

Figs 71.6–11. Heads of Tephritidae, lateral views: (6) *Ceratitoides nigromaculatus* Hendel; (7) *Oedaspis reducta* Freidberg & Kaplan; (8) *Oedoncus taeinipalpis* Speiser; (9) *Xenodorella mira* Munro; (10) *Cryptophorellia elegantula* Freidberg & Hancock; (11) *Orthocanthoides aristae* Freidberg ♀ (inset: ♂ arista). Figs 7–9 (Freidberg & Kaplan 1992, figs 2–4), Fig. 10 (after Freidberg & Hancock 1989, fig. 1), Fig. 11 (after Freidberg 1987, fig. 1).

Abbreviations: ar – arista; fr s – frontal setae; lbl – labellum; oc s – ocellar setae; orb s – orbital seta(e); poc s – postocellar seta; pocl s – postocular setae; vt s – vertical seta.

of *Acanthiophilus* Becker (Tephritini), *Cryptophorellia* Freidberg & Hancock (Axiothaumini) (Figs 184–188) and *Tephritomyia* Hendel (Tephritini) by Morgulis *et al*. (2015), Freidberg & Hancock (1989) and Morgulis *et al*. (2016), respectively, while the biology of gall-formers was discussed by Freidberg (1984: 129, 1998: 36) and Munro (1952). Mating behaviour in *Schistopterum* Becker (Schistopterini) and *Metasphenisca* Hendel (Tephrellini) was reported by Freidberg (1981, 1986, 1997). Final instar larvae of many species, particularly the fruit infesters, have the ability to "jump", by flexing the abdomen, thus enabling them to distance themselves from their rotting hosts (or escape from predators) when on the ground. Pupariation by fruit infesters is normally in the ground, but some *Dacus* species pupariate in asclepiad pods, *Notomma* Bezzi in their twig galls, *Coelopacidia* Enderlein and *Zacerata* Coquillett within stems and most Tephritinae species within their galls or flower heads. The habit of communal roosting in *Dacus* during winter or cool weather, involving multiple species, was noted by Munro (1984) and discussed by Hancock (1989: 54).

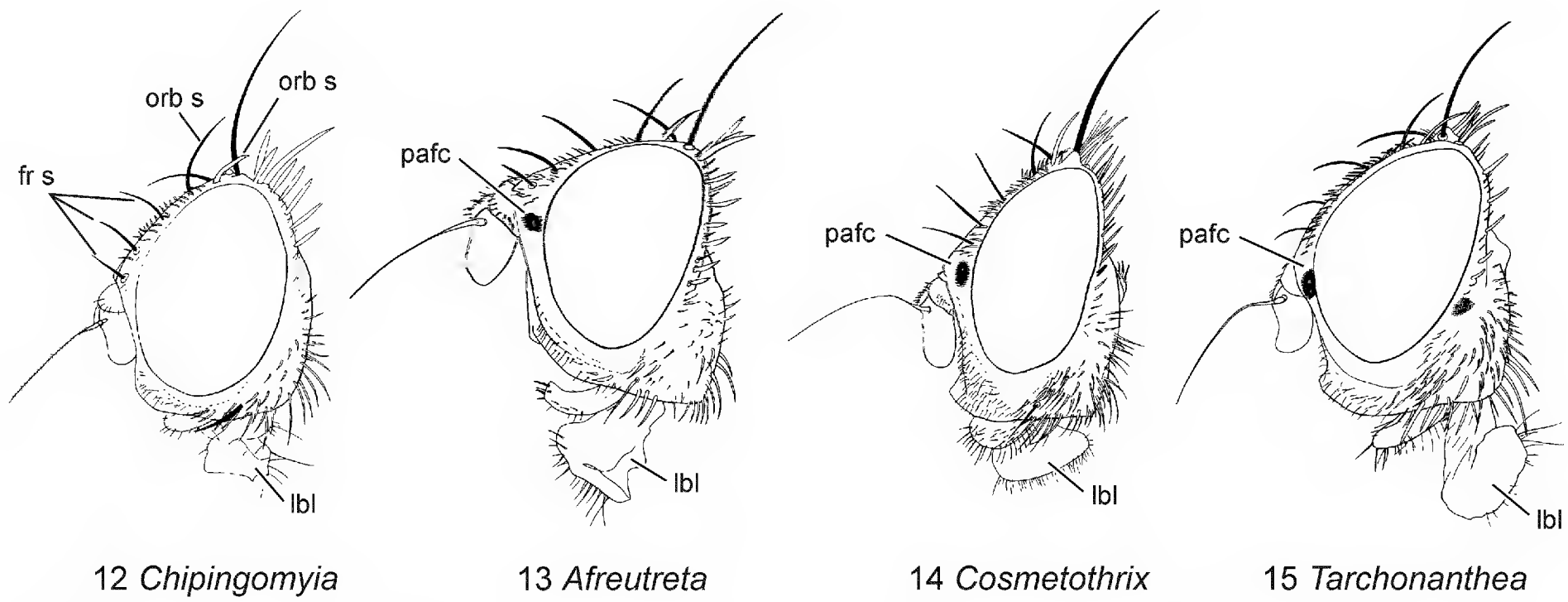
Males of many Dacinae species are attracted to synthetic pheromones or "lures". Pioneering studies were undertaken by Ripley & Hepburn (1931, 1935) and, since then, the attractants terpinyl acetate, trimedlure (tert-butyl (4/5) chloro-2-methylcyclohexane carboxylate), methyl eugenol, cue-lure (4-(p-acetoxyphenol)-2-butanone) and vert-lure (methyl- or propyl-p-hydroxybenzoate) have been found to be useful in detecting and monitoring populations of *Bactrocera* Macquart, *Ceratitis* and *Dacus* species in the Afrotropics (Hancock 1985*b*, *c*, 1987), particularly those of economic importance. Many species of Tephritinae are attracted to bright yellow pan traps.

At least some tephritids appear to play a role in pollination. In Asia, New Guinea and northern Australia, *Bactrocera* species are frequently attracted to orchids and occasionally trapped with orchid pollinia attached to their eyes or scutum (Clarke *et al*. 2002; D.L. Hancock, pers. obs.). Similarly, Afrotropical *Dacus* species, including cucurbit-feeders, have been found with asclepiad pollinia attached to their tarsi (Hancock & Drew 2006; Munro 1984).

Economic significance

Tephritidae include some of the world's most damaging horticultural pests, with the most serious placed in subfamily Dacinae. In the Afrotropical Region, several species of *Dacus* are pests of cucurbits, while *Bactrocera* and *Ceratitis* attack a wide range of fruits. At least four species of Asian *Bactrocera* have become adventive in the region, with one, *B*. (*B*.) *invadens* Drew, Tsuruta & White, 2005, having spread throughout most of sub-Saharan Africa and the Malagasy subregion. Note that some authors do not agree that *B. invadens* is a distinct species (of Indian origin) and much recent literature treats it under the name *B. dorsalis* (Hendel, 1912), an East Asian species adventive in Hawaii. Larvae feed on bacteria introduced during oviposition, causing the fruit to rot. A few species of *Trirhithrum* attack coffee and, while the bean itself is generally not infested, the taste is reportedly sometimes unpleasantly affected by the introduction of a *Xanthomonas*-type bacterium (Le Pelley 1968: 247). Several pest species were discussed by Hancock (1989: 51), but reports of *Dacus* (*Dacus*) *bivittatus* (Bigot, 1858), attacking coffee in São Tomé Is. result from a misas-sociation of *Ceratitis* (*Ceratitis*) *capitata* (Wiedemann, 1824) larvae in fruit with *D*. (*D*.) *bivittatus* adults in traps; this and several erroneous records of *Trirhithrum* from coffee and cocoa were noted by Hancock & White (1997). A list of recorded host-plants for *Ceratitis* species was provided by De Meyer *et al*. (2002).

A few species of the primarily Asteraceae-feeding subfamily Tephritinae have been deliberately introduced to various countries as biocontrol agents for noxious weeds, including *Procecidochares utilis* Stone, 1947, in South Africa, while some other species are regarded as minor pests of cultivated flowers, such



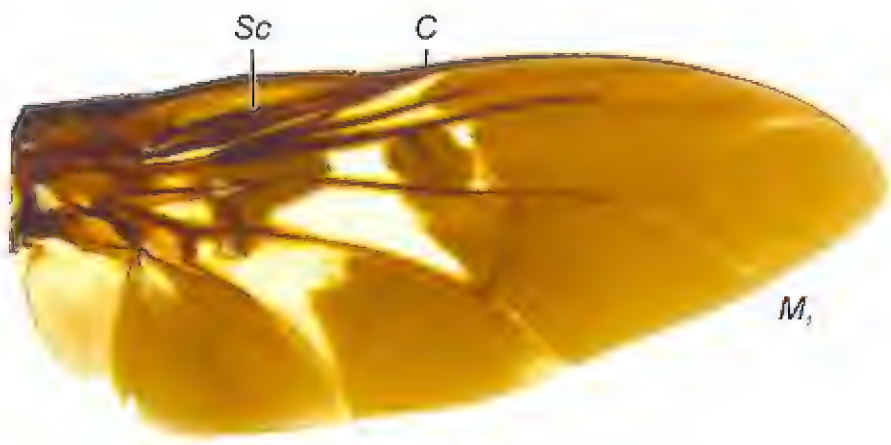
Figs 71.12–15. Heads of Tephritidae (lateral views): (12) *Chipingomyia manica* Hancock; (13) *Afreutreta bipunctata* (Loew); (14) *Cosmetothrix discoidalis* (Bezzi); (15) *Tarchonanthea coleoptrata* Freidberg & Kaplan. Figs 12–15 (after Freidberg & Kaplan 1993, figs 8, 1, 4, 5, respectively).

Abbreviations: fr s – frontal setae; lbl – labellum; orb s – orbital seta; pafc – parafacial.

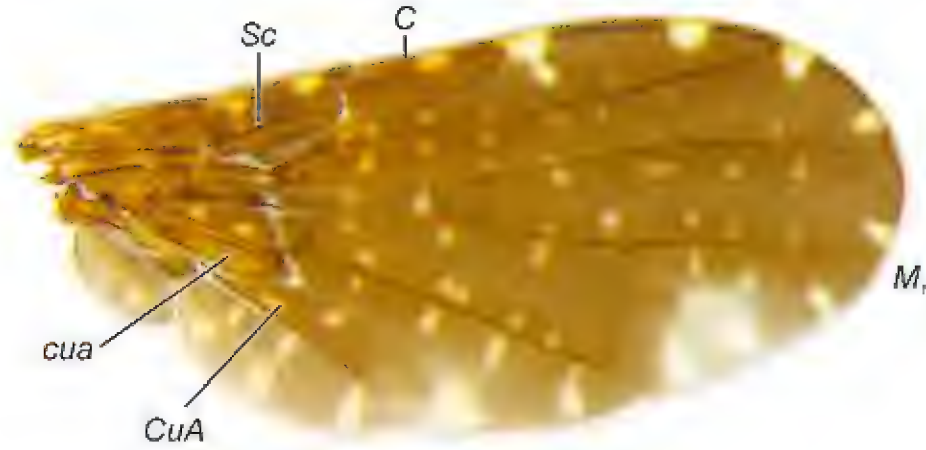
as Barberton daisies. *Acanthiophilus helianthi* (Rossi, 1794), is a major pest of Safflower, *Carthamus tinctorius* L. (Asteraceae), causing up to 70% seed loss in some areas (Morgulis *et al*. 2015). *Zacerata asparagi* Coquillett, 1924 (Zaceratini) infests stems of wild asparagus and has occasionally been recorded from cultivated varieties. *Coelopacidia vivax* (Munro, 1933) (Trypetinae: Adramini) was recorded as a pest of cultivated *Cineraria* (Asteraceae: Senecioneae) in South Africa by Munro (1960).

Classification

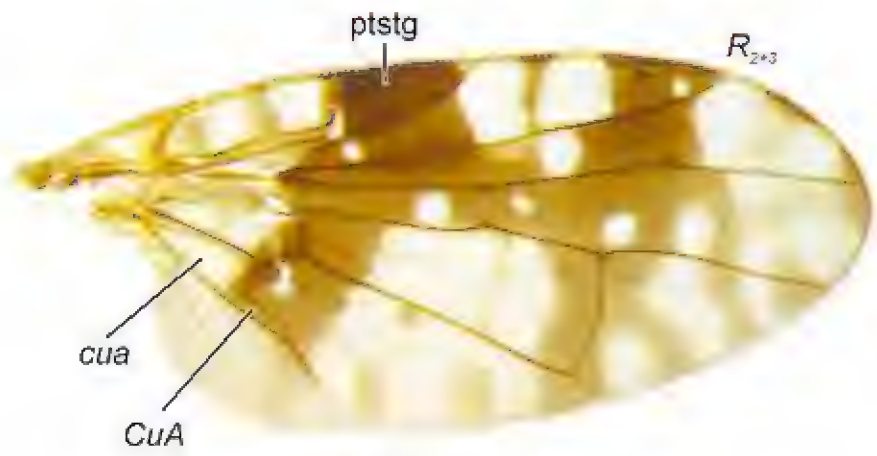
Tephritidae is one of eight families included in the superfamily Tephritoidea by Korneyev (1999*a*: 3), the other seven being the Lonchaeidae, Piophilidae, Platystomatidae, Pyrgotidae, Ulidiidae and the non-Afrotropical families Pallopteridae and Richardiidae. Two additional families, Ctenostylidae and Eurygnathomyiidae (non-Afrotropical), were included by Han & Ro (2016), the Ctenostylidae having been added by Korneyev (2015). The subfamily and tribal classification of Tephritidae in current use was largely proposed by Korneyev (1999*b*: 549) and includes six subfamilies: Blepharoneurinae, Dacinae, Phytalmiinae, Tachiniscinae, Tephritinae and Trypetinae; all of which occur in the Afrotropical Region. The former subfamily Zaceratinae is treated here as a tribe within Tephritinae. The convoluted history and composition of the subfamily Trypetinae was discussed by Hancock (1986*a*).



16 *Bibundia*

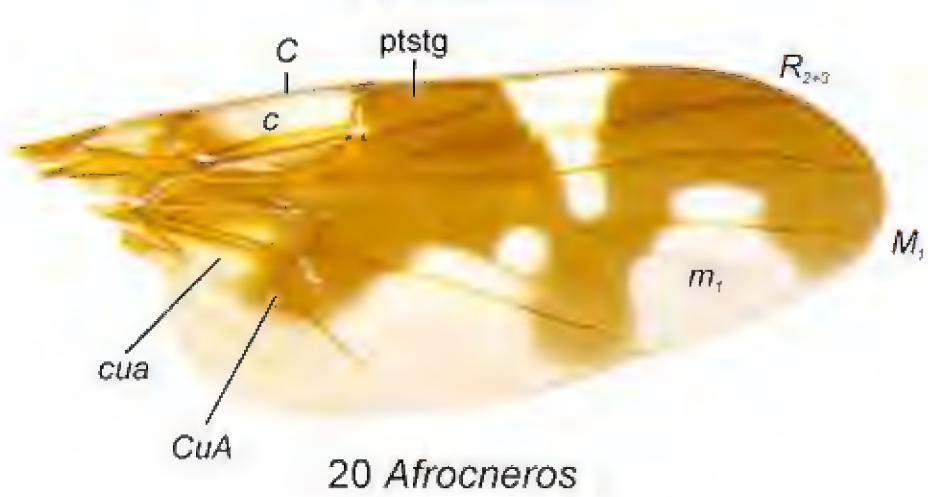


17 *Baryglossa*

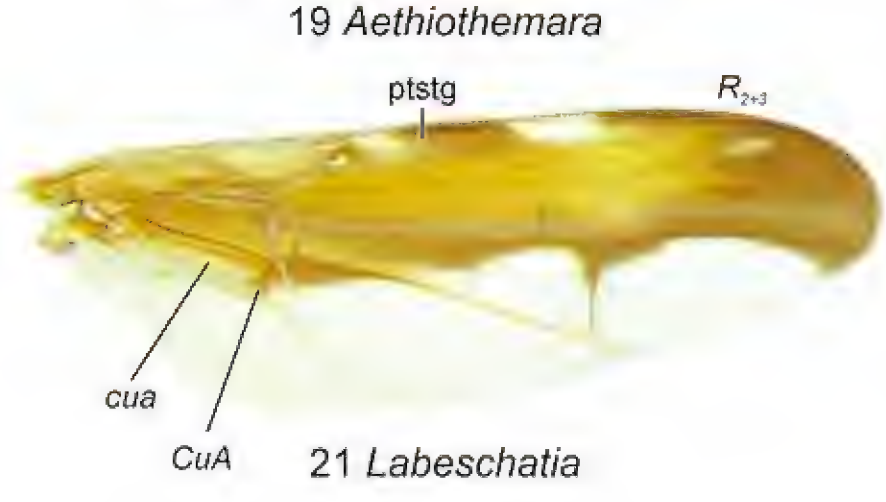


18 *Baryglossa*

19 *Aethiothemara*



20 *Afrocneros*



21 *Labeschatia*

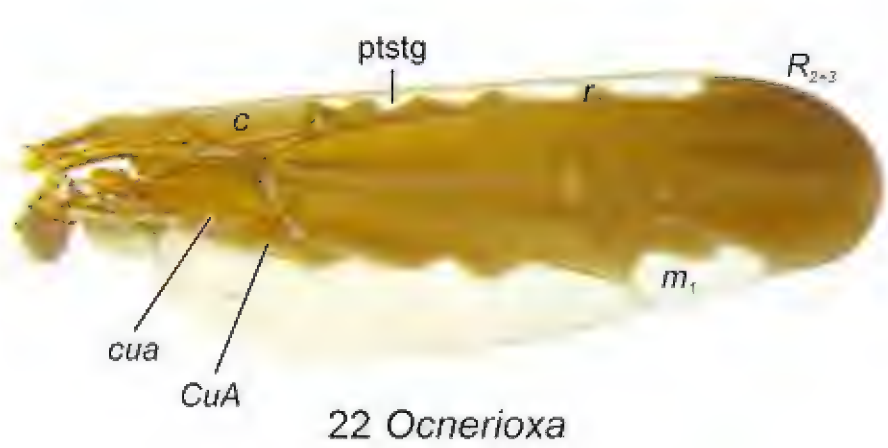
Figs 71.16–21. Wings of Tephritidae (dorsal views): (16) *Bibundia fenestrata* Grünberg; (17) *Baryglossa bequaerti* Bezzi; (18) *B. trulla* Munro; (19) *Aethiothemara fallacivena* (Enderlein); (20) *Afrocneros excellens* (Loew); (21) *Labeschatia circumlineata* Munro.

Abbreviations: *c* – costal cell; *C* – costal vein; *CuA* – anterior branch of cubital vein; *cua* – anterior cubital cell; M_1 – first branch of media; m_1 – first medial cell; ptstg – pterostigma; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *Sc* – subcostal vein.

Blepharoneurinae is regarded as one of the earliest-branching subfamilies. Larvae develop in flowers, fruit, seeds or stems of Cucurbitaceae. Only the genus *Baryglossa* Bezzi occurs in the Afrotropical Region. Relationships of the five included genera (one an amber fossil from Dominican Republic), were reviewed by Norrbom & Condon (1999: 135).

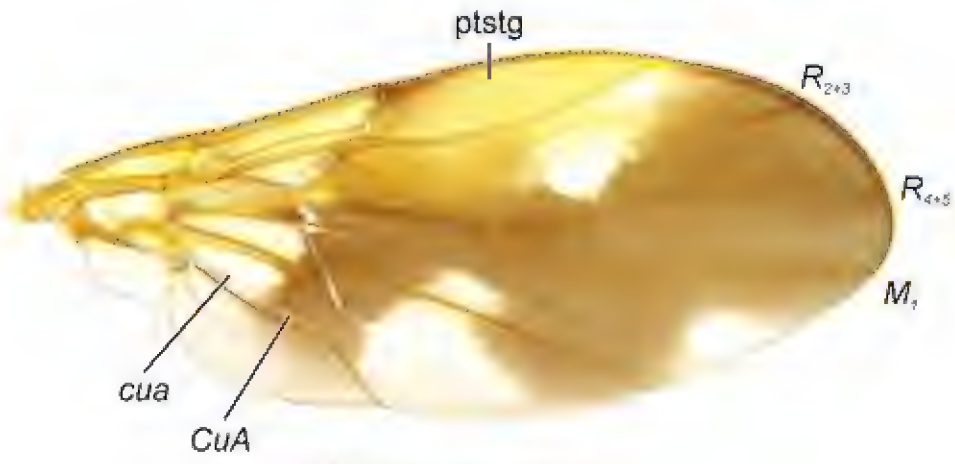
Dacinae comprises three tribes: Ceratitidini, Dacini and Gastrozonini, all of which occur in the Afrotropics. Larvae develop primarily in fruit and some, particularly in the speciose genera *Bactrocera*, *Ceratitis* and *Dacus*, are among the most notorious of horticultural pests. Species of Gastrozonini, however, develop in grasses (Poaceae), including bamboo shoots. Fifteen Afrotropical genera are recognised, nine in Ceratitidini (Hancock & White 1997), two in Dacini (Hancock & Drew 2006; White 2006) and four in Gastrozonini (Hancock 1999). The subfamily includes the following Afrotropical tribes and genera: Ceratitidini – *Capparimyia* Bezzi, *Carpophthoromyia* Austen, *Ceratitis*, *Eumictoxenus* Munro, *Neoceratitis* Hendel, *Nippia* Munro, *Perilampsis* Bezzi, *Trirhithrum* and *Xanthorrachista* Hendel; Dacini – *Bactrocera* (including *Zeugodacus* Hendel, sometimes recognised as a separate genus) and *Dacus*; Gastrozonini – *Bistrispinaria* Speiser, *Ceratitoides* Hendel, *Clinotaenia* Bezzi and *Leucotaeniella* Bezzi. The subgeneric classifications of *Ceratitis* and *Dacus* were discussed by Hancock (1984) and Hancock & Drew (2006), respectively.

Phytalmiinae is regarded as another of the early branching subfamilies (Korneyev 1999*b*: 94). Larvae are primarily saprophagous, feeding in rotting parenchymatous tissue beneath tree bark, in fruit or (in some Oriental groups) in decaying bamboo shoots or culms. Six Afrotropical genera are recognised: *Aethiothemara* Hendel, *Afrocneros* Bezzi, *Labeschatia* Munro, *Ocnerioxa* Speiser, *Ptiloniola* Hendel and *Themarictera* Hendel,



22 *Ocnerioxa*

23 *Ptiloniola*



24 *Themarictera*

25 *Coelopacidia*

26 *Coelotrypes*

27 *Coelotrypes*

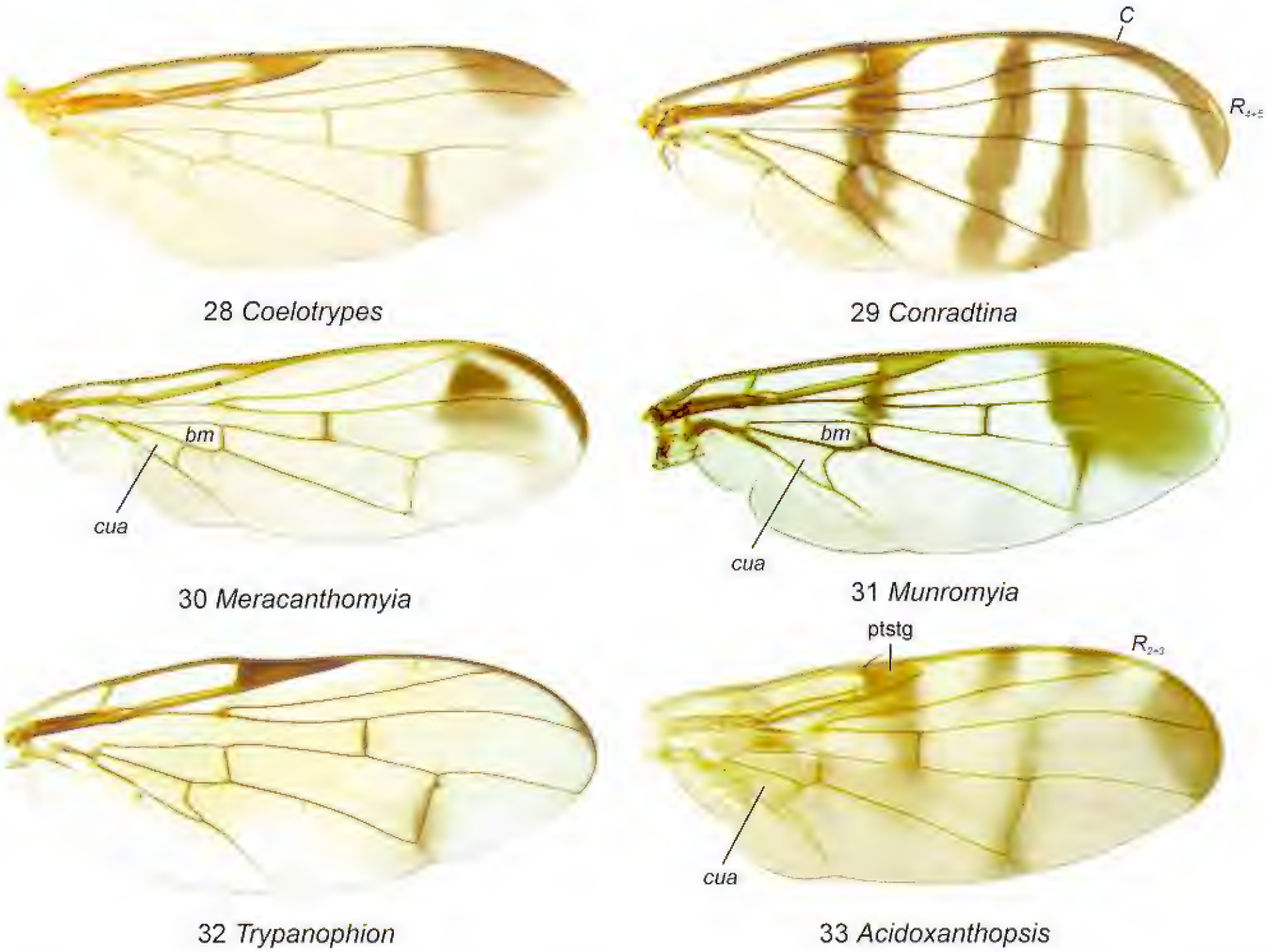
Figs 71.22–27. Wings of Tephritidae (dorsal views): (22) *Ocnerioxa pennata* Speiser; (23) *Ptiloniola tripunctulata* (Karsch); (24) *Themarictera flaveolata* (F.); (25) *Coelopacidia punctum* (Enderlein); (26) *Coelotrypes major* (Bezzi); (27) *C. pulchellinus* (Hering).

Abbreviations: *c* – costal cell; *CuA* – anterior branch of cubital vein; *cua* – anterior cubital cell; M_1 – first branch of media; m_1 – first medial cell; ptstg – pterostigma; r_1 – first radial cell; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius.

all placed in the endemic *Aethiothemara*-group in the tribe Acanthonevrini (Hancock 1986*a*, 2015).

Tachiniscinae is often treated as a separate family, but is included here within the Tephritidae, following the study of Korneyev (1999*a*: 13, *b*: 92). Larvae are believed to be parasitic on larvae or pupae of saturniid moths (Lepidoptera), although only one species has actually been reared. Two Afrotropical genera are recognised: *Bibundia* and *Tachiniscidia* Malloch, both included in the tribe Tachiniscini. The subfamily was revised by Korneyev & Norrbom (2006) and is regarded as the earliest-branching of the subfamilies.

Tephritinae is the largest and possibly most derived of the subfamilies and is exceptionally diverse in the Afrotropics. Korneyev (1999*c*: 549) recognised 10 tribes, an unplaced Palaearctic genus and two groups of genera: Cecidocharini, Myopitini, Noeetini, Terelliini and Xyphosiini, plus the *Axiothauma*- and *Tomoplagia*-groups in the "lower Tephritinae" and Dithrycini, Eutretini, Schistopterini, Tephrellini, Tephritinae and the unplaced Palaearctic genus *Acinia* Robineau-Desvoidy in the "higher Tephritinae". The tribe Axiothaumini was established by Hancock (2003*a*) for the *Axiothauma*-group, but *Terpnodesma* Munro was later removed, due to an incorrect diagnosis (Hancock 2006*a*). Two additional tribes are included here: Pliomelaenini and Zaceratini. The tribe Pliomelaenini (established by Munro (1937) as "Platensinini", a name now known to apply to the Dithrycini as a subtribe and regarded as a senior synonym of Oedaspidina (Hancock 2001)), was treated as a separate tribe by Hancock *et al*. (2003). Sometimes regarded as a subtribe of Tephrellini, based on a shared use of Acanthaceae as host-plants, the different groups of host genera utilised suggest homoplasy and, until their relationships are better understood, they are best kept separate; it is possible that the Pliomelaenini represents no more than a group of genera (*Pliomelaena*-group)



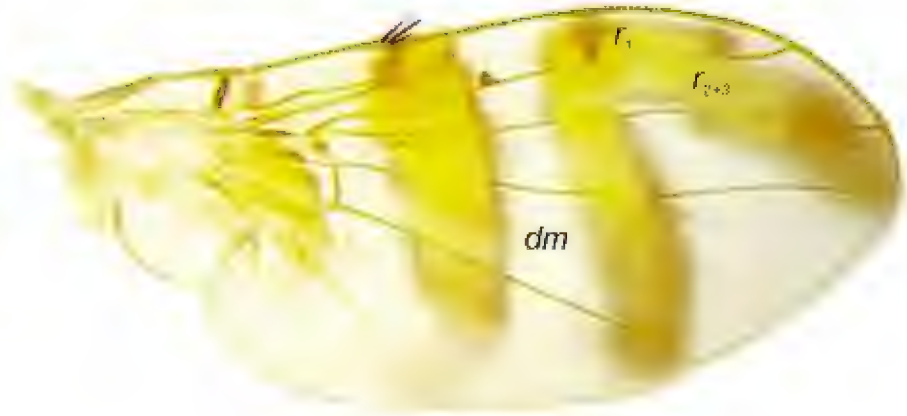
Figs 71.28–33. Wings of Tephritidae (dorsal views): (28) *Coelotrypes vittatus* Bezzi; (29) *Conradtina longicornis* Enderlein; (30) *Meracanthomyia antennata* (Hendel); (31) *Munromyia nudiseta* Bezzi; (32) *Trypanophion gigas* Bezzi; (33) *Acidoxanthopsis advena* Hering.

Abbreviations: *bm* – basal medial cell; *C* – costal vein; *cua* – anterior cubital cell; ptstg – pterostigma; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius.

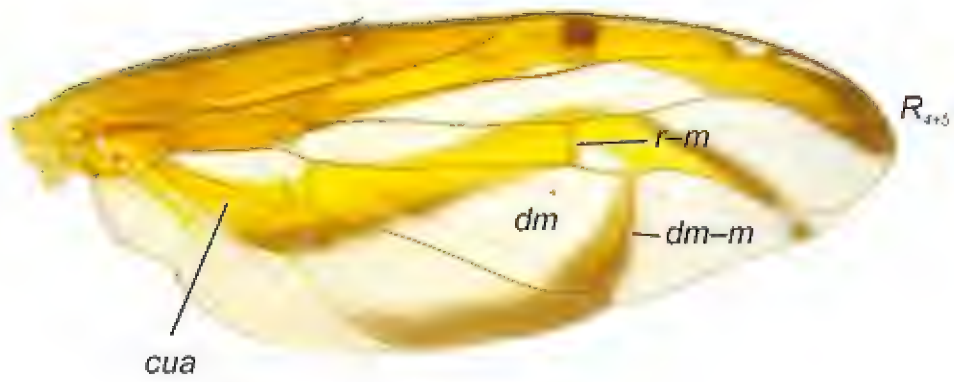
within the tribe Tephritini. The tribe Zaceratini was proposed by Hancock (1986*a*) as a tribe in the subfamily Trypetinae, but was later shown to be the sister-group to the subfamily Tephritinae by both Han & McPheron (1999: 122) and Korneyev (1999*c*: 550), based on molecular and morphological analyses, respectively. It is treated here as an early branching tribe within the Tephritinae and includes only two monotypic genera, the Afrotropical *Zacerata* and the Palaearctic *Plioreocepta* Korneyev (Korneyev 1999*c*: 550). Larvae of most Tephritinae develop in flower heads, seeds or stems of Asteraceae, Acanthaceae, Lamiaceae and Verbenaceae; many are gall-formers. Larvae of Zaceratini, however, mine the stems of *Asparagus* (Liliaceae).

Twelve tribes and 114 valid genera of Tephritinae occur in the Afrotropics, with the 48 genera of Tephritini placed in the introduced (Nearctic/Neotropical) *Euaresta*-group and the widespread *Campiglossa*, *Spathulina*, *Sphenella* and *Tephritis* groups of genera. Tephrellini is also divided into three groups of genera, based on host-plant use: Acanthaceae for the *Metasphenisca*-group, Lamiaceae for the *Aciura*-group and Verbenaceae for the *Munroella*-group. Several Afrotropical tribes, or groups, have been extensively reviewed or revised: Tephrellini and Pliomelaenini by Munro (1947), the *Campiglossa* and *Sphenella* groups of the Tephritini by Munro (1957*a*, *b*), Tephrellini by Hancock (1990), Eutretini by Freidberg & Kaplan (1993), Myopitini by Freidberg & Norrbom (1999: 581), the *Tephritis*-group

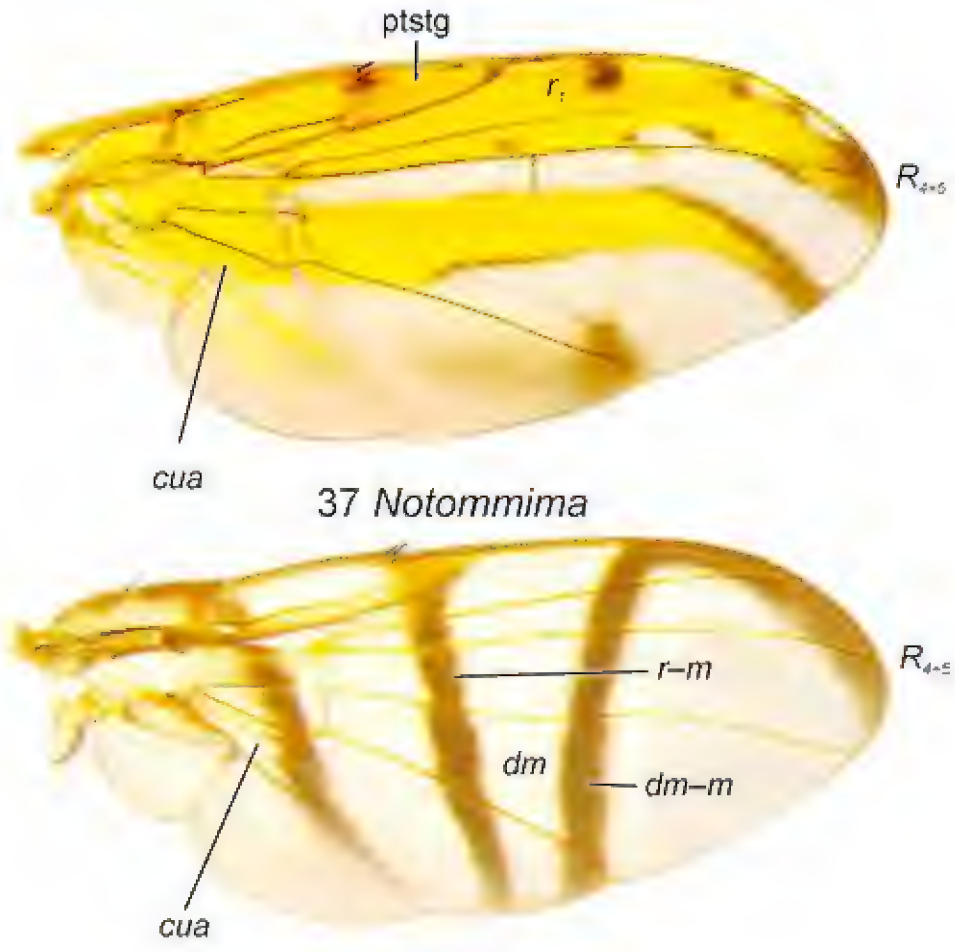
34 *Sosiopsila*



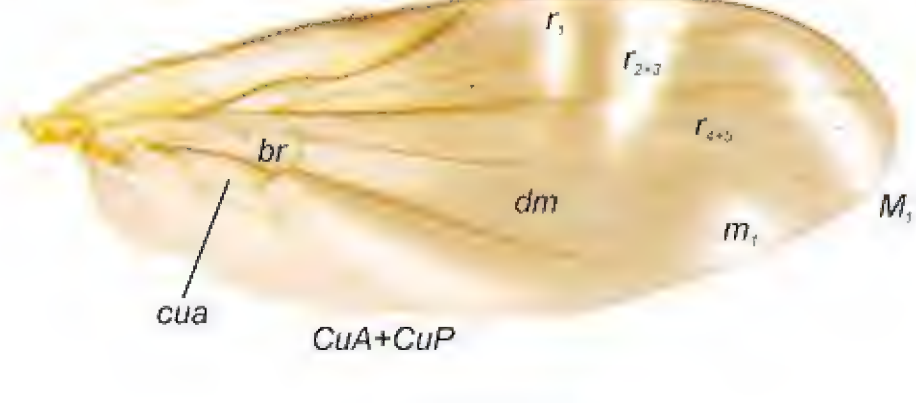
35 *Myiopardalis*



36 *Notomma*



37 *Notommima*



38 *Ochrobapha*

39 *Scleropithus*

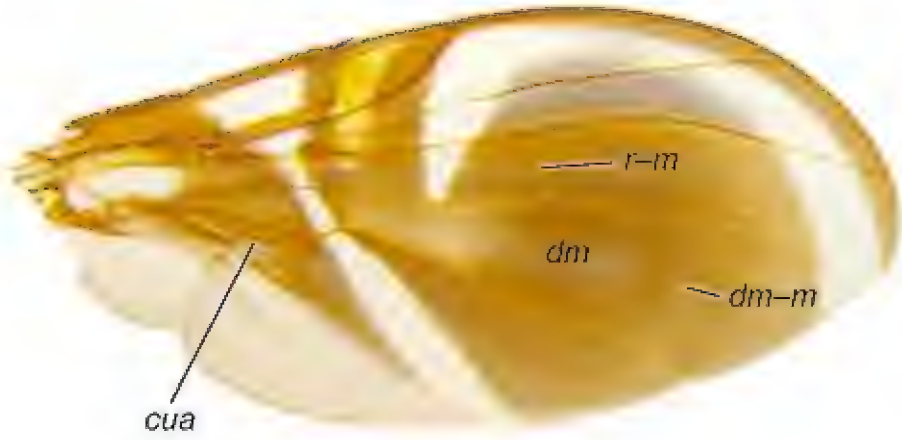
Figs 71.34–39. Wings of Tephritidae (dorsal views): (34) *Sosiopsila metadacus* (Speiser); (35) *Myiopardalis pardalina* (Bigot); (36) *Notomma bioculatum* Bezzi; (37) *Notommima parallela* Freidberg & Copeland; (38) *Ochrobapha pallescens* Munro; (39) *Scleropithus glaphyrochalyps* Munro.

Abbreviations: *br* – basal radial cell; *C* – costal vein; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *dm* – discal medial cell; *dm–m* – discal medial crossvein; M_1 – first branch of media; m_1 – first medial cell; ptstg – pterostigma; r_1 – first radial cell; r_{2+3} – second + third radial cell; r_{4+5} – fourth + fifth radial cell; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein.

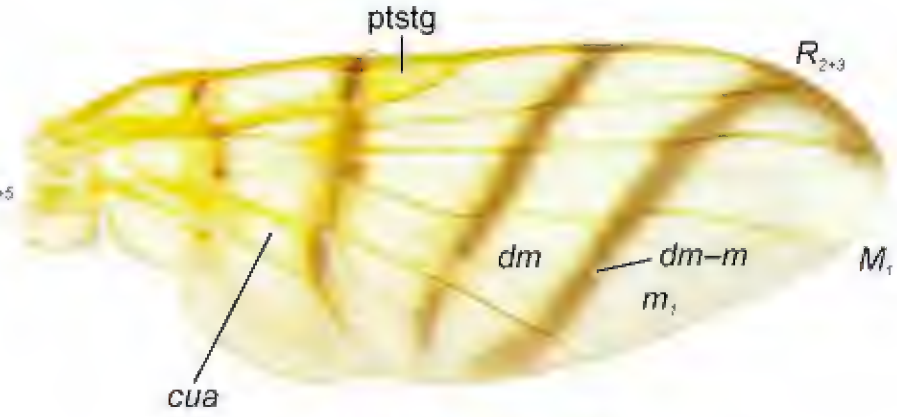
of the Tephritini by Merz (1999: 629) and Schistopterini by Freidberg (2002). Tribes and genera are detailed below:

"Lower Tephritinae": Zaceratini – *Zacerata*; Terelliini – *Craspedoxantha* Bezzi; Myopitini – *Asimoneura* Czerny, *Myopites* Blot, *Spinicosta* Freidberg & Norrbom, *Stamnophora* Munro and *Urophora* Robineau-Desvoidy; Axiothaumini – *Axiothauma* Munro, *Cryptophorellia* and *Orthocanthoides* Freidberg; Noeetini – *Ensina* Robineau-Desvoidy; Cecidocharini – the introduced *Procecidochares* Hendel.

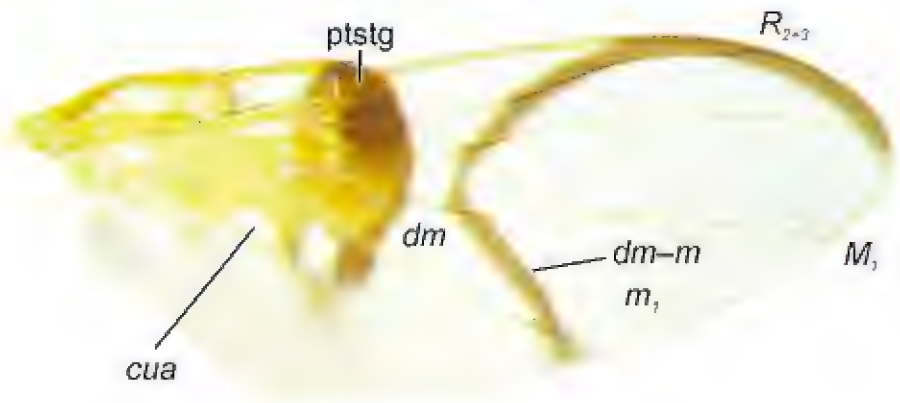
"Higher Tephritinae": Dithrycini (Platensinina) – *Euthauma* Munro and *Oedaspis* Loew; Eutretini – *Afreutreta* Bezzi, *Cosmetothrix* Munro, *Perirhithrum* Bezzi and *Tarchonanthea* Freidberg & Kaplan; Schistopterini – *Bactropota* Bezzi, *Brachiopterna* Bezzi, *Clematochaeta* Hering, *Cordylopteryx* Hering, *Eutretosoma* Hendel, *Heringomyia* Hardy, *Melanopterella* Freidberg, *Microtreta* Freidberg, *Rhabdochaeta* de Meijere, *Rhochmopterum* Speiser, *Schistopterum*, *Schistotephritis* Freidberg and *Setoides* Zonstein & Freidberg and *Tanzanimyia* Freidberg, Zonstein & Friedman; Tephrellini: *Aciura* group of genera – *Aciura* Robineau-Desvoidy, *Dicheniotes* Munro, *Gymnaciura* Hering, *Katonaia* Munro, *Oxyaciura* Hendel, (*Parasphenisca* Hendel not yet recorded, but might occur), *Sphaeniscus* Becker and *Ypsilomena* Munro; *Metasphenisca* group of genera – *Brachyaciura* Bezzi, *Dorycricus* Munro, *Malagaciura* Hancock, *Metasphenisca*,



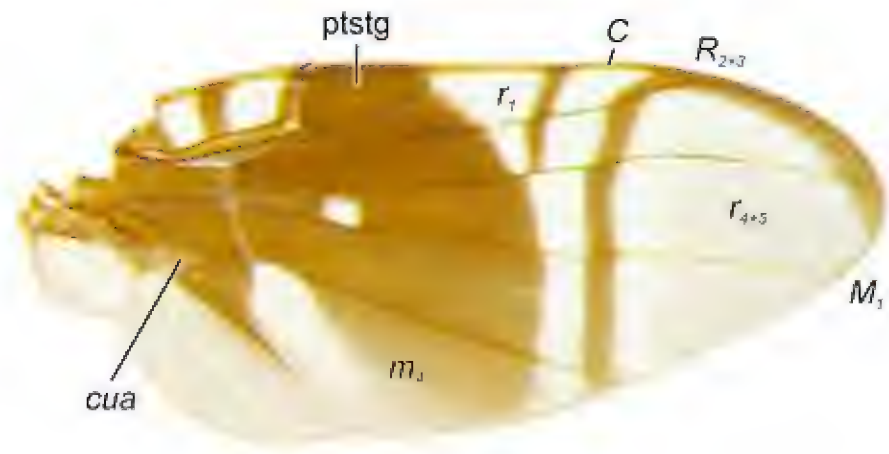
40 *Taomyia*



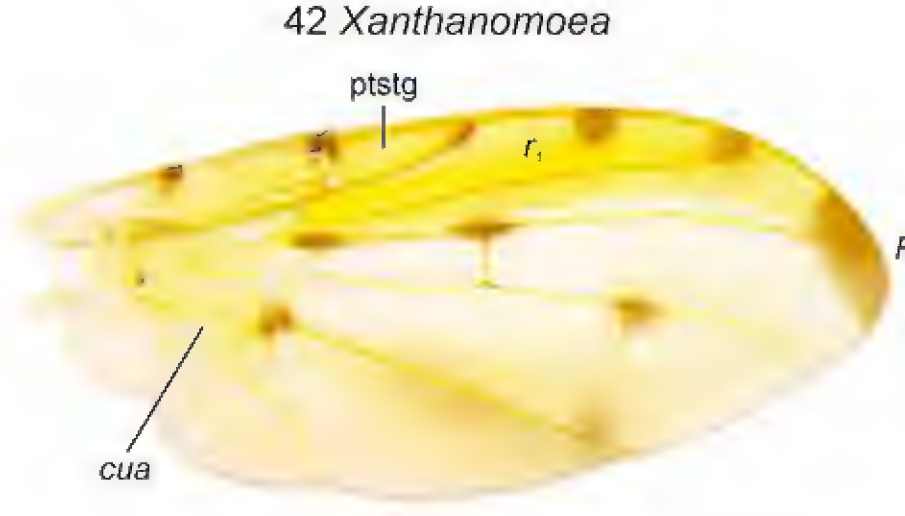
41 *Rivelliomima*



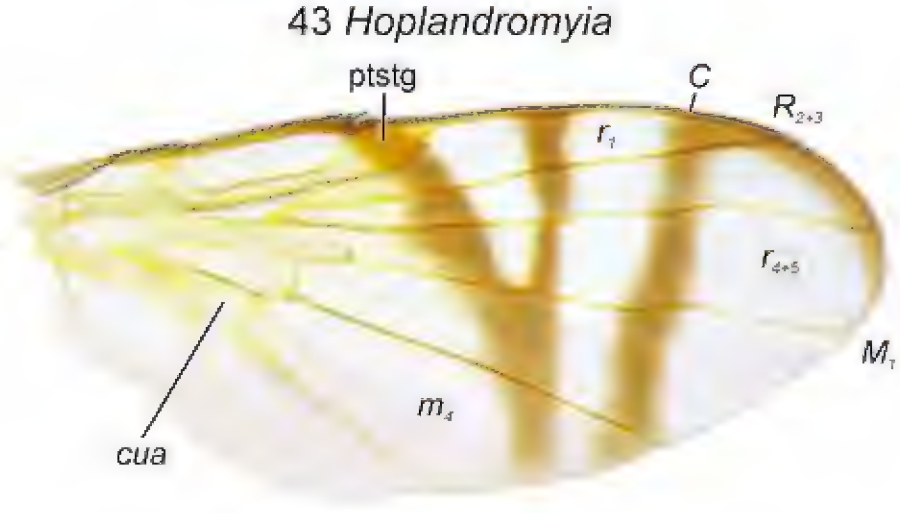
42 *Xanthanomoea*



43 *Hoplandromyia*



44 *Notommoides*



45 *Pseudomyoleja*

Figs 71.40–45. Wings of Tephritidae (dorsal views): (40) *Taomyia marshalli* Bezzi; (41) *Rivelliomima punctiventris* Bezzi; (42) *Xanthanomoea munroi* Bezzi; (43) *Hoplandromyia madagascariensis* Hancock; (44) *Notommoides albida* Freidberg; (45) *Pseudomyoleja nigricans* Han & Freidberg.

Abbreviations: *C* – costal vein; *cua* – anterior cubital cell; *dm* – discal medial cell; *dm–m* – discal medial crossvein; M_1 – first branch of media; m_1 – first medial cell; m_4 – fourth medial cell; ptstg – pterostigma; r_1 – first radial cell; R_{2+3} – second branch of radius; r_{4+5} – fourth + fifth radial cells; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein.

Ocnerioxyna Séguy, *Oedoncus* Speiser, *Paraciura* Hering, *Pycnella* Munro and *Tephraciura* Hering; *Munroella* group of genera – *Afraciura* Hering, *Munroella* Bezzi and *Parasphenisciodes* Hering; Pliomelaenini – *Bezzina* Munro, *Chipingomyia* Hancock, *Deroparia* Munro, *Elaphromyia* Bezzi, *Euryphalara* Munro, *Ghentia* Munro, *Hyaloctoides* Munro, *Leucothrix* Munro, *Manicomyia* Hancock, *Platomma* Bezzi, *Pliomelaena* Bezzi, *Psednometopum* Munro, *Pseudafreutreta* Hering, *Pterope* Munro, *Stephanotrypeta* Hendel, *Triandomelaena* Hancock and *Xenodorella* Munro.

Tribe Tephritini: *Campiglossa* group of genera – *Antoxya* Munro, *Campiglossa* Rondani, *Desmella* Munro, *Dioxyna* Frey, *Lethyna* Munro, *Mastigolina* Munro, *Mesoclanis* Munro, *Namwambina* Munro, *Pediapelta* Munro, *Ptosanthus* Munro, *Scedella* Munro and *Tanaica* Munro; *Euaresta* group of genera – the introduced *Euaresta* Loew; *Spathulina* group of genera – *Elgonina* Munro, *Gymnosagena* Munro, *Marriottella* Munro, *Migmella* Munro, *Peratomixis* Munro, *Spathulina* Rondani and *Tephritoresta* Hering; *Sphenella* group of genera – *Acronneus* Munro, *Oedosphenella* Frey (incl. *Bevismyia* Munro), *Parafreutreta* Munro, *Paratephritis* Shiraki, *Sphenella* Robineau-Desvoidy and *Telaletes* Munro; *Tephritis* group of genera – *Acanthiophilus* Becker, *Actinoptera* Rondani, *Arabodesis* Merz & Dawah, *Brachydesis* Hancock, *Brachytrupanea* Hancock, *Capitites* Foote & Freidberg, *Dectodesis* Munro, *Euarestella* Hendel, *Freidbergia* Merz, *Goniurellia* Hendel, *Hyalotephritis* Freidberg, *Insizwa* Munro, *Multireticula* Merz, *Pherothrinax* Munro, *Stelladesis* Merz, *Tephritis* Latreille, *Tephritomyia* Hendel, *Tephrodesis* Merz, *Trupanea* Schrank and *Trupanodesis* Merz.

Trypetinae was included in the "higher Tephritidae" by Korneyev (1999*b*: 103), who recognised eight tribes: Adramini, Carpomyini, Hexachaetini, Nitrariomyiini, Rivelliomimini, Toxotrypanini, Trypetini and Xarnutini. Two additional tribes are recognised here: Acidoxanthini, treated tentatively as a subtribe of Nitrariomyiini by Korneyev (1999*b*: 107), but of uncertain relationships; and Callistomyiini, proposed by Hancock (2007*c*) to include two Oriental/Australasian genera and, provisionally, the Afrotropical genus *Sosiopsila* Bezzi, left unplaced by Korneyev (1999*b*: 106). The proposed tribal classification of Hancock (1986*a*) was extensively revised and improved by Korneyev (1999*b*: 73) and the tribe Trypetini was treated in detail by Han (1999: 253). Larvae are primarily fruit- or seed-feeders, but some, particularly in the tribe Trypetini, are leaf-miners. Six tribes and 25 genera are recorded from the Afrotropical Region, with most reviewed by Hancock (1986*a*, 2005, 2007*c*, 2019). Two otherwise Oriental/Australasian genera, *Acidoxantha* Hendel (Acidoxanthini) and *Hemilea* Loew (Trypetini), are represented in the Afrotropics by single species in Madagascar (Hancock 1985*a*). The subfamily includes the following Afrotropical tribes and genera: Callistomyiini – *Sosiopsila*; Rivelliomimini – *Rivelliomima* Bezzi and *Xanthanomoea* Bezzi; Adramini – *Celidodacus* Hendel, *Coelopacidia*, *Coelotrypes* Bezzi, *Conradtina* Enderlein, *Meracanthomyia*, *Munromyia* Bezzi, *Soita* Walker and *Trypanophion* Bezzi; Carpomyini – *Carpomya* Costa, *Myiopardalis* Bezzi (sometimes included in *Carpomya*), *Notomma*, *Notommima* Freidberg & Copeland, *Ochrobapha* Munro, *Scleropithus* Munro and *Taomyia* Bezzi; Acidoxanthini – *Acidoxantha* and *Acidoxanthopsis* Hering; Trypetini – *Hemilea*, *Hoplandromyia* Bezzi, *Notommoides* Hancock, *Philophylla* Rondani, *Pseudomyoleja* Han & Freidberg.

Identification

No identification key to all known Afrotropical genera of Tephritidae has been published since that of Bezzi (1924*a*). The identification key in this chapter is in part a compilation of the partial keys published by various authors, such as Merz (1999: 659), Munro (1947, 1957*a*, *b*), and the writers (see "Literature cited" below). Wing patterns (Figs 16–176) are important identifying features at both generic and specific levels, but some genera, particularly in the Tephritinae, are complex and in these cases generic determinations should be checked against revisions of the genera concerned. Some additional head characters are illustrated in Figs 7–15. One atypical species, *Actinoptera vinsoni* Munro, 1946, from Mauritius, keys to *Euarestella* and further study of its generic position is required. *Bevismyia* is included within *Oedosphenella*. The placement of an undescribed genus from Madagascar (Fig. 144) is uncertain and it is not included in the key. Tephritidae are best micro-pinned in the field for later double-mounting (see Chapter 2).

Key to genera of Afrotropical Tephritidae

1. Subcostal wing vein (*Sc*) gradually curved forward, reaching costal vein (*C*); costal vein ending before vein M_1 (e.g., Fig. 16) and scutellum with > 4 pairs of marginal setae; antennal arista bare; pedicel long, > 2 × length of postpedicel (= first flagellomere); oviscape with dorsoapical opening (TACHINISCINI) 2
– Subcostal wing vein (*Sc*) turned sharply forward at apex, not reaching costal vein (*C*); costal vein reaching vein M_1 (e.g., Fig. 17), if ending before, then scutellum with only 1 or 2 pairs of marginal setae, or antennal arista plumose, or pedicel short, not longer than postpedicel; female oviscape opened posteroapically (e.g., Fig. 182) 3
2. Bumblebee-mimicking flies; abdomen round, flattened with tergites fused; scutellum with > 9 pairs of marginal setae; head without ocelli and frontal setae; antennal pedicel 4 × as long as wide. . . . . *Bibundia* Bischof
– Wasp-mimicking flies; abdomen elongate-oval with tergites separated; scutellum with 5 pairs of marginal setae; head with ocelli and 3 frontal setae; antennal pedicel > 10 × as long as wide. . . . . *Tachiniscidia* Malloch

3. Wing with basal medial cell (*bm*) subrectangular, base > 2 × width of anterior cubital cell (*cua*) (e.g., Figs 46, 47); cell *cua* longer than cell *bm*, apex drawn-out into long acute extension (e.g., Figs 46, 47); thorax without postpronotal, presutural, dorsocentral and katepisternal setae, other setae weak (DACINI) 4

– Wing with basal medial cell (*bm*) subtriangular, base *ca* as wide as anterior cubital cell (*cua*), acute; cell *cua* at most slightly longer than cell *bm*, apex blunt (e.g., Fig. 71) or with short to moderate extension (e.g., Figs 30, 31, 51); thorax usually with postpronotal, presutural, dorsocentral and katepisternal setae, most setae well-developed. 19

4. All abdominal tergites fused; thorax without prescutellar acrostichal setae . . . . . *Dacus* F. *sensu lato* 5

– Abdominal tergites 3–5 not fused; thorax usually with prescutellar acrostichal setae . . . . . *Bactrocera* Macquart *sensu lato* 15

5. Wing with basal costal cell (*bc*) and costal cell (*c*) fuscous, with dense microtrichia over entire costal cell (*c*) and often part of cell *bc*; costal band broad, but not expanded into large apical macula or crossing vein M_1; scutum without postsutural yellow vittae; abdomen distinctly petiolate and club-shaped (restricted to Madagascar). . . . . *Dacus* (*Neodacus* Perkins)

– Not as above; if wing with basal costal cell (*bc*) and costal cell (*c*) fuscous, with dense microtrichia over at least entire costal cell (*c*), then either costal band expanded into large apical macula crossing vein M_1 or scutum with postsutural yellow vittae present and abdomen elongate-oval, not distinctly petiolate (not restricted to Madagascar) 6

6. Scutum with yellow triangular mark on transverse suture joined to normally yellow notopleural lobe; wing with costal band expanded into large apical macula crossing vein M_1; anal streak (fuscous stripe in anterior cubital cell (*cua*) alongside vein *CuA+CuP*) distinct; 3, 1 or no postsutural yellow vittae, if 1 or none, then wing with either basal costal cell (*bc*) and costal cell (*c*) fuscous, with dense microtrichia over at least all of cell *c*, or apical macula not covering most of basal ½ of cell r_{4+5} . . . . . *Dacus* (*Mictodacus* Munro) [in part]

– Scutum not as above, if with yellow triangular mark on transverse suture, none or 1 postsutural yellow vitta, distinct anal streak and apical macula crossing vein M_1, then basal costal cell (*bc*) and costal cell (*c*) without microtrichia over at least all of cell *c* and apical macula occupies all or most of basal ½ of cell r_{4+5} 7

7. Scutum with yellow triangular mark on transverse suture joined to normally yellow notopleural lobe; scutum with medial postsutural yellow vitta; face either black on upper ¾, yellow below, or yellow with 2 black maculae, wing with diffuse fuscous discal area . . . . . *Dacus* (*Mictodacus* Munro) [in part]

– Scutum with yellow mark on transverse suture often reduced to isolated macula or absent; face often entirely yellow, if largely black, then scutum without yellow mark on transverse suture; if face yellow with 2 black maculae, then scutum without medial postsutural yellow vitta and wing without diffuse fuscous discal area 8

8. Scutum with yellow mark on transverse suture reduced to isolated macula or absent, with 0–3 postsutural yellow vittae, all narrow; wing with anal streak; costal band not expanded into large apical macula reaching vein M_1 or, if so and weakly crossing it, then crossvein *r–m* also infuscated and scutum with only medial postsutural vitta; if mark on transverse suture absent, then face yellow with 2 black maculae and supra-alar setae present. . . . . *Dacus sensu stricto*

– Not as above; medial postsutural yellow vitta, if present, often broadened posteriorly; supra-alar setae usually absent, if present, then face entirely yellow or, if face yellow with 2 black maculae, then costal band expanded into large apical macula reaching vein M_1 and scutum with 3 postsutural yellow vittae; anal streak often much reduced or absent 9

9. Scutum with supra-alar setae (includes *D. chrysomphalus* (Bezzi, 1924) and species formerly placed in *Metidacus* Munro) . . . . . *Dacus* (*Leptoxyda* Macquart) [in part]

– Scutum without supra-alar setae 10

10. Scutum with fine, white pubescence; medial postsutural yellow vitta broadly oval to pyriform or reduced to short stripe from just posterior to transverse suture; either with face mostly black, wing with microtrichia absent in cell *br* anterior to cell *bm*, costal band absent beyond apex of vein R_{2+3} and anal streak absent; or with face yellow, microtrichia present, costal band narrow beyond apex of vein R_{2+3} and anal streak much reduced . . . . . *Dacus* (*Lophodacus* Collart)

– Scutum not as above, with medial postsutural vitta narrow and triangular, broad and transverse (and situated posteriorly), or absent; face yellow or with 2 black maculae; if yellow, then scutum without postsutural yellow vittae and/or anal streak absent 11

11. Scutum with yellow mark on transverse suture joined to notopleural lobe or absent; medial postsutural yellow vitta often present, if absent then: (A), fore tarsi with apical segment enlarged; or (B), face, postpronotal lobe and scutellum yellow, yellow mark on suture absent, costal band expanded into large apical macula crossing vein M_1 and anal streak absent; or (C), face with 2 black maculae, yellow mark on suture joined to notopleural lobe but narrow, costal band expanded basally or apically and anal streak very pale or absent. . . . . *Dacus* (*Leptoxyda* Macquart) [in part]

– Not as above; medial postsutural vitta absent; costal band neither expanded basally nor with large apical macula 12

12. Head with face entirely yellow. 13

– Head with face yellow with 2 black maculae 14

13. Wing without costal band, but with isolated apical macula; without microtrichia in cell *br* anterior to cell *bm* (*D. scaber*-group, including species formerly placed in *Saccodacus* Munro) . . . . . *Dacus* (*Didacus* Collart) [in part]

– Wing with or without costal band; with microtrichia extensive in cell *br* anterior to cell *bm* . . . . . *Dacus* (*Psilodacus* Collart) [in part]

14. Scutum with yellow mark on suture triangular (sometimes narrow or vestigial), joined to notopleural lobe; anterior notopleural seta present, but often weak; wing with costal band narrow and fuscous, not crossing vein R_{2+3} except at apex; cells *bc* and *c* hyaline; microtrichia in cell *br* anterior to cell *bm* extensive; *r–m* crossvein not infuscated; anal streak distinct; anatergite and katatergite not both fuscous; fore, mid and hind femora not dark, dark and partly dark, respectively; male abdominal tergite 3 with pecten of cilia; female terminalia with aculeus apically pointed . . . . . *Dacus* (*Didacus* Collart) [in part]

– Not as above; yellow mark on thoracic suture variable, often reduced or absent; anterior notopleural seta sometimes absent; wing with costal band sometimes pale or reduced with isolated apical macula; microtrichia in cell *br* anterior to cell *bm* extensive, reduced to narrow stripe or absent; *r–m* crossvein sometimes infuscated; anal streak distinct, weak or absent; anatergite and katatergite sometimes both fuscous; femoral colour variable; male abdominal tergite 3 with pecten of cilia often vestigial or absent; female terminalia with aculeus apically variable, sometimes blunt, notched, lobed or serrate . . . . . *Dacus* (*Psilodacus* Collart) [in part]

15. Thorax with anatergite yellow 16

– Thorax with anatergite red-brown to black. 18

16. Wing broadly fuscous in apical ½, with darker medial band enclosing both *r–m* and *dm–m* crossveins; face yellow, not maculate; male wing with distinct supernumerary lobe posteriorly (as in Fig. 47) (restricted to Madagascar) . . . . . *Bactrocera* (*Aglaodacus* Munro)

– Wing mostly hyaline, without dark medial band enclosing both *r–m* and *dm–m* crossveins; face with pair of black maculae; male wing with or without distinct supernumerary lobe posteriorly (not restricted to Madagascar) 17

17. Scutum with medial postsutural yellow vitta; wing with isolated infuscation over *dm–m* crossvein (Fig. 47); male wing with distinct supernumerary lobe posteriorly (Fig. 47); male abdominal sternite 5 not deeply indented posteriorly; surstylus with elongate and finger-like posterior lobe . . . . . *Bactrocera* (*Javadacus* Hardy)

– Scutum without medial postsutural yellow vitta; wing without isolated infuscation over *dm–m* crossvein (Fig. 46); male wing with at most weak supernumerary lobe posteriorly (Fig. 46); male abdominal sternite 5 deeply indented posteriorly; surstylus with short, blunt posterior lobe . . . . . *Bactrocera sensu stricto*

18. Scutum with supra-alar setae; male abdominal tergite 3 without pecten of distinct setulae. . . . . *Bactrocera* (*Gymnodacus* Munro)

– Scutum without supra-alar setae; male abdominal tergite 3 with pecten of distinct setulae. . . . . *Bactrocera* (*Daculus* Speiser)

19. Thorax with anatergite with long and thin pale trichia (ADRAMINI) 20

– Thorax with anatergite bare or with very short microtrichia 27

20. Head and thorax with ocellar, postocular, postpronotal, presutural, dorsocentral and katepisternal setae all absent; femora spinose ventrally; antennae much longer than face 21

– Head and thorax with ocellar, postocular, postpronotal, presutural, dorsocentral and katepisternal setae not all absent; femora often not spinose ventrally; antennae often shorter than face. 22

21. Antennal arista plumose; scutellum with 1 pair of marginal setae . . . . . *Meracanthomyia* Hendel

– Antennal arista bare; scutellum with 2 pairs of marginal setae . . . . . *Munromyia* Bezzi

22. Wing vein M_4 setulose dorsally; antennae longer than face; thoracic mesosternum with numerous short, spine-like setae in anterior ½ . . . . . *Soita* Walker

– Wing vein M_4 bare; antennae shorter than face; thoracic mesosternum without numerous short spine-like setae in anterior ½ 23

23. Fore and mid femora ventrally spined; scutum with presutural supra-alar setae 24

– Fore and mid femora not ventrally spined; scutum without presutural supra-alar setae 25

24. Wing with apical portion largely dark, with hyaline apical macula; apical section of vein R_{4+5} straight; scutum with prescutellar acrostichal setae . . . . . *Celidodacus* Hendel

– Wing with apical portion largely hyaline, with dark band along costal vein (*C*) (Fig. 29); apical section of vein R_{4+5} curved posteriorly (Fig. 29); scutum normally without prescutellar acrostichal setae . . . . . *Conradtina* Enderlein

25. Thorax without distinct anepisternal seta; scutellum with 1 pair of marginal setae . . . . . *Trypanophion* Bezzi

– Thorax with distinct anepisternal seta; scutellum with 2 pairs of marginal setae 26

26. Mid tibia with 2 apical spurs; hind femur without row of dorsal setae; thorax with dorsocentral setae weak or absent . . . . . *Coelopacidia* Enderlein

– Mid tibia with 1 apical spur; hind femur with row of dorsal setae; thorax with dorsocentral setae present. . . . . *Coelotrypes* Bezzi

27. Head and thorax with ocellar, postocular, postpronotal, presutural, dorsocentral and katepisternal setae all absent; wing with anterior cubital cell (*cua*) blunt, not drawn-out at posterior apex (Fig. 34); abdomen elongate (CALLISTOMYIINI) . . . . . *Sosiopsila* Bezzi

– Head and thorax with ocellar, postocular, postpronotal, presutural, dorsocentral and katepisternal setae not all absent; wing with anterior cubital cell (*cua*) often drawn-out at posterior apex (e.g., Figs 64, 65); abdomen oval, rounded or subtriangular 28

28. Scutum usually with scapular setae (e.g., Fig. 5), if these rudimentary or absent, then ocellar setae minute and presutural, supra-alar, prescutellar acrostichal, anepimeral and katepisternal setae all absent; head with postocular setae slender and black unless other setae pale; scutum usually with dark microtrichia and dorsocentral setae usually placed posterior to line of supra-alar setae, rarely anterior; wing with costal seta often not well-developed; cell *cua* usually with distinct apical extension 29

– Scutum without scapular setae, at least outer pair, or not differentiated from row of long, coarse setulae; postocular setae often thickened and whitish; scutum usually clothed in fine, pale microtrichia and dorsocentral setae usually placed anterior to line of supra-alar setae; wing with costal seta usually well-developed; cell *cua* often with apical extension very short or absent (TEPHRITINAE [in part]) 75

29. Wing vein *CuA* sinuous (e.g., Figs 49–67), apical section distal to crossvein *m–cu* weakly or distinctly bowed, such that cell *cua* extension broader medially than subbasally (e.g., Figs 49–67); wing cells *c*, *br*, *bm* and *cua* often with distinct brown maculae and scutum often with distinct yellow postsutural vittae (GASTROZONINI & CERATITIDINI). 30

– Wing vein *CuA* with apical section angled or virtually straight, not weakly or distinctly bowed (e.g., Figs 17–24); cell *cua* extension broader subbasally than medially (e.g., Figs 17–24); wing cells *c*, *br*, *bm* and *cua* without distinct brown maculae and scutum usually without distinct yellow vittae 47

30. Wing with 3 long black costal setae anterior to apex of subcostal vein (*Sc*) (Fig. 65); scutellum with quadrate basomedial yellow patch . . . . . *Bistrispinaria* Speiser

– Wing with at most 2 distinct black costal setae anterior to apex of subcostal vein (*Sc*) (e.g., Fig. 64); scutellum variable, but without quadrate basomedial yellow patch. 31

31. Wing with 2 short but distinct black costal setae anterior to apex of subcostal vein (*Sc*) (Fig. 64); abdominal tergite 2 (broad posterior part of fused tergites 1 + 2) enlarged, at least 2 × as long as tergite 3. . . . . *Ceratitoides* Hendel

– Wing with (at most) 1 distinct black costal seta anterior to apex of subcostal vein (*Sc*) (e.g., Fig. 63); abdominal tergite 2 (broad posterior part of fused tergites 1 + 2) *ca* as long as tergite 3 32

32. Wing bands mostly yellow, longitudinal, without transverse band across basal part of discal medial cell (*dm*) (Fig. 63); head with well-developed lower occipital swellings, neck set low, head thus raised considerably over front border of thorax; scutum and scutellum with small black maculae. . . . . *Xanthorrachista* Hendel

– Wing either with transverse band across basal part of discal medial cell (*dm*) or pattern much reduced or diffuse, not longitudinal, often brown (e.g., Figs 55, 56); head normal, with lower occipital swellings not well-developed; scutum and scutellum often with large (rarely small) black maculae 33

33. Antennal pedicel spinulose or with coarse black setulae 34

– Antennal pedicel neither spinulose nor with coarse black setulae 37

34. Wing pattern not distinctly banded (e.g., Figs 55, 56), often weakly reticulate; scutellum entirely whitish or yellow 35

– Wing pattern distinctly banded or banded/reticulate (e.g., Figs 66, 67), scutellum with at least apical black macula, often 3 and sometimes virtually or entirely black 36

35. Scutum with extensive silvery tomentose medial area and distinct black maculae; wing cell *bc* brown (Fig. 55); head with occiput with weak ventral swellings. . . . . .*Eumictoxenus* Munro

– Scutum without silvery areas or distinct black maculae; wing cell *bc* hyaline (Fig. 56); head with occiput flat, without ventral swellings . . . . . *Nippia* Munro

36. Scutum brownish black to black, if largely fulvous in male, then black areas present dorsocentrally in posterior part; scutellum with 3 large black maculae or largely or entirely black, apical macula quadrate; postnotum shiny blackish brown to black; abdomen with transverse black bands at least on tergite 3 . . . . . .*Clinotaenia* Bezzi

– Scutum fulvous, with pair of black maculae posterolaterally; scutellum with 1 or 3 small black maculae, the apical small and semicircular; postnotum fulvous to red-brown; abdomen fulvous to brown, without black bands . . . . . *Leucotaeniella* Bezzi

37. Scutum and abdomen usually dark reddish to brown or black; scutum sometimes with greyish pubescence in central areas, but without prescutellar yellow or white areas, often metallic blue, green or purple with silvery areas in Malagasy species; wing bands usually well-developed, but pattern diffuse in some males, blackish brown without yellow areas; wing with basal area often without distinct maculae and streaks in cells *c*, *br*, *bm* and *cua*; medial band across end of vein M_1 usually present, at least as tooth from costal band (e.g., Figs 48, 57, 59–62); scutellum often mostly or entirely yellow or black or with yellow basal band 38

– Scutum and abdomen usually fulvous to brown; scutum usually with darker streaks or maculae and usually with paired, yellow or white prescutellar maculae or bands; wing bands often yellow or with yellow areas; if scutum mostly black with greyish pubescence and wing bands entirely brown, then yellow or white prescutellar maculae or fascia invariably present; wing with basal area usually with distinct maculae and streaks in cells *c*, *br*, *bm* and *cua*, if these absent, then wing pattern much reduced; medial band across end of vein M_1 often present only near hind margin of wing or absent (e.g., Figs 49–55); scutellum usually yellow with black markings, apical black area often trilobed or divided into 3 large quadrate maculae, the yellow sometimes reduced to narrow basal band or maculae in dark-bodied species 41

38. Wing band across *dm–m* crossvein parallel to that over *r–m* crossvein, joined or convergent with medial band over end of vein M_1 (Fig. 48), if largely fused with band over crossvein *r–m* and costal band, then with large, triangular hyaline indentation across apex of cell *sc*; thorax with 2 anepisternal setae and head usually with 3 frontal setae; anepisternum with distinct yellow or white fascia; postpronotal lobe white to yellow or (rarely) pale brown . . . . . .*Carpophthoromyia* Austen

– Wing band across *dm–m* crossvein, when present, not parallel to band over *r–m* crossvein, usually joined or convergent with that band, occasionally directed towards costal band, but not joined or convergent with medial band across end of vein M_1 (e.g., Figs 57–62); without large, triangular hyaline indentation across apex of cell *sc*; thorax usually with 1 anepisternal seta and head with 2 frontal setae, if 2 anepisternal and 3 frontal setae, then anepisternum and postpronotal lobe black. 39

39. Thorax with anepisternum, anatergite and katatergite broadly yellow or white; scutum extensively greyish pubescent; scutellum black, with broad or narrow basal yellow band or maculae; postpronotal lobe partly or entirely yellow or white; antennal arista with very short pubescence . . . *Neoceratitis* Hendel

– Thorax with anepisternum normally with at most single narrow whitish line along upper margin, if broadly white or yellow, then either postpronotal lobe black or scutellum either entirely black or yellow, or with black areas reduced to 3 posterior marginal maculae; anatergite and katatergite usually mostly or entirely black; scutum not extensively greyish pubescent; antennal arista often with long pubescence 40

40. Thorax with broad, diagonal, yellow or white band across postpronotal lobe and anepisternum; scutellum usually entirely yellow or white, rarely black apically; wing usually with medial band, if reduced to

tooth, then costal band narrowed and hyaline band across cell *c* broad, reaching hind margin of wing (Fig. 59) . . . . . *Perilampsis* Bezzi

– Thorax with postpronotal lobe at least partly black and anepisternum rarely with broad, diagonal pale band, if so, then postpronotal lobe entirely black; scutellum with 3 black marginal maculae or largely or entirely black, rarely entirely yellow; wing with medial band often reduced to tooth but costal band not narrowed (Figs 60–62) . . . . . *Trirhithrum* Bezzi

41. Scutellum with apical black area bilobed or comprised of 2 large maculae with yellow medial line between them . . . . . *Capparimyia* Bezzi

– Scutellum with apical black area trilobed or comprised of 3 usually large, quadrate maculae, rarely all black or with 5 small black maculae (Fig. 2) . . . . . *Ceratitis* MacLeay *sensu lato* 42

42. Wing pattern reduced to isolated apical macula in cell r_{4+5}, posterior to apex of vein R_{4+5}; wing apex produced, especially in male (Fig. 49); discal medial cell (*dm*) distinctly broadened, especially in male; *r–m* crossvein directed towards apex of subcostal cell (*sc*) (Fig. 49); scutum fulvous, without distinct black maculae; abdomen fulvous without black band or maculae on tergite 3 . . . . . *Ceratitis* (*Acropteromma* Bezzi)

– Wing pattern normally distinctly banded, if reduced to isolated maculae, then apical macula situated in cell r_{2+3} anterior to apex of vein R_{4+5}; wing apex not produced; discal medial cell (*dm*) not distinctly broadened; *r–m* crossvein directed towards apex, middle or base of subcostal cell (*sc*) (Figs 50–54); scutum fulvous to black, with or without distinct black maculae; abdomen with or without black band or maculae on tergite 3 43

43. Thorax with 2 anepisternal setae; postpronotal lobe not maculate; scutum red-brown to brown, with darker streaks, but no distinct black maculae; wing bands mostly brown (Fig. 53); scutellum with 3 large, quadrate apical maculae; abdomen with pattern of weak or distinct dark lateral and medial maculae on tergites 2–5 and submedial patches on anterior margins of tergites 3–5; frons with silvery or golden areas . . . . . *Ceratitis* (*Pardalaspis* Bezzi)

– Thorax with 1 anepisternal seta, if 2, then wing bands mostly yellow (e.g., Figs 50–52); postpronotal lobe often maculate; scutum often with large black maculae; scutellum variously marked; abdomen rarely maculate, if so, then not as above; frons with or without silvery areas 44

44. Abdominal tergite 3 with brownish black to black band of variable width; scutum usually without distinct black maculae 45

– Abdomen fulvous, without black band on tergite 3; scutum usually with distinct black maculae 46

45. Wing bands mostly yellow; cubital band angled towards *r–m* crossvein, but separate; medial band across end of vein M_1 weakly or distinctly connected to costal band (Fig. 52); head with 2 (some females) or 3 well-developed frontal setae, in male on slightly elevated ridge ("cristate"); male mid legs and fore femur unmodified; head with frons silvery . . . . . *Ceratitis* (*Hoplolophomyia* Bezzi)

– Wing bands mostly brown; pattern variable, sometimes reduced to small isolated patches (Fig. 54); head with frontal setae not cristate; male mid legs often feathered or fore femur patterned black and white; head with frons not silvery. . . . . *Ceratitis* (*Pterandrus* Bezzi)

46. Wing broad (Fig. 51); costal band generally separate from basal band, if not, then cubital band separate from basal band (Fig. 51) and either antennal arista plumose or scutellum with apical black area not divided into 3; males usually with anterior orbital seta incrassate, or with terminal process; legs often with orange feathering; thorax with postpronotal lobe maculate; with 1 anepisternal seta . . . . . *Ceratitis sensu stricto*

– Wing narrow (Fig. 50); not with the above combination of characters; anterior orbital seta unmodified; thorax with postpronotal lobe often not maculate; with 1 or 2 anepisternal setae . . . . . *Ceratitis* (*Ceratalaspis* Hancock)

47. Wing with pterostigma elongate, at least slightly so; wing vein R_{2+3} often sinuous (e.g., Figs 19–24); head with ocellar setae rudimentary or absent; scutellum with 2 or 3 pairs of marginal setae, if 2, then thorax without anepimeral seta, if 3, then antennal arista pubescent or plumose; female aculeus with sub-apical setae (ACANTHONEVRINI) 48

– Wing with pterostigma short (e.g., Figs 18, 33, 42–45) and/or head with ocellar setae well-developed; wing vein R_{2+3} straight (e.g., Figs 18, 33, 42–45); scutellum with 1, 2 or 3 pairs of marginal setae, if 2, then thorax with anepimeral seta, if 3, then antennal arista bare; female aculeus without sub-apical setae 53

48. Scutellum with 3 pairs of marginal setae, the medial pair often thin and weak; antennal arista long-plumose 49

– Scutellum with 2 pairs of marginal setae; antennal arista short-plumose to bare 50

49. Thorax with katepisternal seta well-developed; scutellum with medial marginal seta not weaker than outer pair; wing veins R_{4+5} and M_1 divergent apically (Fig. 19); head < 2 × (*ca* 1.6 ×) as broad as long in both sexes; legs with erect long, thin setae; female aculeus not pointed apically. . . . . *Aethiothemara* Hendel

– Thorax with katepisternal seta weak or absent; scutellum with medial marginal seta weaker than outer pair; wing veins R_{4+5} and M_1 with apical sections parallel (Fig. 24); head > 2 × as broad as long (*ca* 3.5 × in male, 2.3 × in female); legs without erect long, thin setae; female aculeus pointed apically. . . . . *Themarictera* Hendel

50. Thorax without presutural, supra-alar, prescutellar acrostichal, anepimeral and katepisternal setae . . . . . *Labeschatia* Munro

– Thorax usually with presutural, supra-alar, prescutellar acrostichal, anepimeral and katepisternal setae (sometimes without presutural and anepimeral setae) 51

51. Head with postocular setae close-set, spaces between setae *ca* 0.15–0.20 × as long as setae; antennal arista short-plumose; thorax with 2 anepisternal setae; wing entirely, or almost entirely, dark brown to black, usually without yellow areas, sometimes with hyaline marginal maculae or with posterior margin largely hyaline; vein R_{2+3} gently undulate opposite end of pterostigma (Fig. 23); female aculeus tactile, apex wide and rounded. . . . . *Ptiloniola* Hendel

– Head with postocular setae not close-set, spaces between setae *ca* 0.5 × as long as setae; antennal arista pubescent or bare, if short-plumose, then thorax with 1 anepisternal seta and wing with transverse hyaline band; wing pattern dimidiate or modified dimidiate, usually with large hyaline areas in posterior ½; vein R_{2+3} straight (e.g., Figs 20, 22); female aculeus variable 52

52. Wing with pterostigma shorter than costal cell (*c*); antennal arista with short pubescence basally, sparse pubescence dorsally; head with face flattened to somewhat concave, slightly swollen ventrally, but ventral facial margin not forming angled ridge; thorax with 2 anepisternal setae; scutellum slightly convex, blackish medially; wing *ca* 2.7 × as long as wide, with 3 hyaline indents, one on costal vein (C) extending below vein R_{2+3}, but separated from indentation in cell m_1 and 2 at hind margin (Fig. 20); female aculeus not strongly pointed . . . . . *Afrocneros* Bezzi

– Wing with pterostigma as long as, or longer than, costal cell (*c*); antennal arista usually with microscopic pubescence or bare; head with ventral facial margin forming angled ridge; thorax with 1 anepisternal seta or with additional weak ventral seta; scutellum flat, triangular and yellow; wing *ca* 3.1 × as long as wide, pattern more or less dimidiate, with hyaline indentation in cell r_1 either not crossing vein R_{2+3}, or forming complete transverse band in cell m_1 (Fig. 22); female aculeus strongly pointed . . . . . *Ocnerioxa* Speiser

53. Thoracic anepisternum with distinct seta anterior to phragma; scutellum with 3 pairs of marginal setae (BLEPHARONEURINI) . . . . . *Baryglossa* Bezzi

– Thoracic anepisternum without distinct seta anterior to phragma; scutellum with 1 or 2 pairs of marginal setae 54

54. Wing with anterior cubital cell (*cua*) apically acute, but not produced into distinct lobe (e.g., Figs 41, 42); head without ocellar setae, other setae fulvous; abdomen with pair of black bullae on tergite 5; female tergite 6 vestigial; body fulvous (RIVELLIOMIMINI) 55

– Wing with anterior cubital cell (*cua*) outwardly curved or inwardly angled, apically blunt or produced into distinct lobe (e.g., Figs 33, 36, 37, 39, 40, 43–45); head with ocellar setae, other setae usually black; abdomen without pair of black bullae on tergite 5; female tergite 6 distinct; body often black 56

55. Wing with discal medial crossvein (*dm–m*) outwardly oblique, posterior angle of discal medial cell (*dm*) blunt; section of vein M_1 above cell *dm* much longer than that over cell m_1; pterostigma longer than wide (Fig. 41). . . . . *Rivelliomima* Bezzi

– Wing with discal medial crossvein (*dm–m*) inwardly oblique, posterior angle of discal medial cell (*dm*) acute; section of vein M_1 above cell *dm* shorter than that over cell m_1; pterostigma very short (Fig. 42) . . . . . .*Xanthanomoea* Bezzi

56. Wing with apical part of vein *CuA* distinctly angled inwardly, anterior cubital cell (*cua*) apically produced into sharp point or lobe (e.g., Fig. 69). 57

– Wing with apical part of vein *CuA* not distinctly angled inwardly, but outwardly curved, anterior cubital cell (*cua*) apically blunt, not produced (e.g., Figs 68, 70–75). 70

57. Head with 2 pairs of frontal setae; wing vein R_{4+5} bare; cell r_1 with 2 hyaline indentations, both extending below vein R_{2+3}; wing bands largely yellow, without medial band, but apical patch well-developed; scutum with black maculae (ACIDOXANTHINI) 58

– Head with 3 pairs of frontal setae; wing vein R_{4+5} often setulose at least at base; cell r_1 with 0–2 hyaline indentations; wing bands often largely pale brown or blackish brown, with medial band often present; scutum often without black maculae (CARPOMYINI & TRYPETINI) 59

58. Wing with 2 sinuous, well-developed, longitudinal bands; *r–m* crossvein beyond middle of discal medial cell (*dm*) (Madagascar) . . . . . *Acidoxantha* Hendel

– Wing bands reduced, not as above; *r–m* crossvein positioned at mid length of discal medial cell (*dm*) (Fig. 33) (East and West Africa) . . . . . *Acidoxanthopsis* Hering

59. Wing with 2 hyaline indentations from costal vein (*C*) in cell r_1, both extending posterior to vein R_{2+3} (e.g., Figs 43, 45) 60

– Wing with 0–1 hyaline indentation from costal vein (*C*) in cell r_1, if 2, then neither extending posterior to vein R_{2+3}, or pattern reduced and wing apex hyaline beyond line of *dm–m* crossvein 62

60. Wing with narrow, dark sub-apical band in cell r_{4+5} crossing tip of vein M_1 . . . . . *Philophylla* Rondani

– Wing without dark sub-apical band in cell r_{4+5}, at most with small macula across apex of vein M_1 (e.g., Figs 43, 45) 61

61. Head with 1 pair of orbital setae; without ocellar setae; frontal setae enlarged, inserted on tubercles in male, normal in female; wing base largely blackish brown, with dark area posterior to pterostigma broadly crossing cell m_4 (Fig. 43); mid tibia with 1 black apical spine; female oviscape much shorter than abdomen . . . . . *Hoplandromyia* Bezzi

– Head with 2 pairs of orbital setae; ocellar setae weakly developed; frontal setae unmodified in both sexes; wing base largely hyaline or fulvous, with dark area posterior to pterostigma forming narrow band across cell m_4 (Fig. 45); mid tibia with 3 distinct black apical spines; female oviscape as long as, or longer than abdomen . . . . . *Pseudomyoleja* Han & Freidberg

62. Thorax with dorsocentral setae inserted well behind line of supra-alar setae, close to prescutellar acrostichal setae 63

– Thorax with dorsocentral setae inserted on, or close to, line of supra-alar setae 67

63. Head and thoracic setae whitish to yellow; body pale, whitish to yellow; wing vein R_{4+5} with extensive setulae (e.g., Figs 37, 44) 64

– Head and thoracic setae dark; body greyish to brownish yellow (often green in life) or blackish brown; wing vein R_{4+5} often with few and sparse setulae (e.g., Figs 36, 39, 40) 65

64. Wing with 2 distinct longitudinal and largely yellow bands, from costal vein (*C*) to vein R_{4+5} (overlapping it apically) and along vein M_1 (Fig. 37) . . . . . *Notommima* Freidberg & Copeland

– Wing largely hyaline or greyish with only pterostigma, costal band and cell r_1 largely yellowish (not along vein M_1) and with darker marginal, apical and discal maculae (Fig. 44) . . . . . *Notommoides* Hancock

65. Wing bands usually longitudinal, partly yellowish; *r–m* crossvein situated near apex of discal medial cell (*dm*), *ca* 1–1.5 × its length from *dm–m* crossvein (Fig. 36) . . . . . *Notomma* Bezzi

– Wing bands transverse, or with large rounded discal patch; *r–m* crossvein situated near middle of discal medial cell (*dm*), *ca* 2 × its length from *dm–m* crossvein (e.g., Figs 39, 40) 66

66. Wing largely hyaline, with 4 slender dark bands, including narrow one from humeral crossvein (*h*) to apex of cell *cua* and two separate bands over *r–m* and *dm–m* crossveins (Fig. 39) . . . . . *Scleropithus* Munro

– Wing with 2 broad, transverse dark bands, including one from humeral crossvein (*h*) to apex of cell *cua* and large rounded discal patch enclosing *r–m* and *dm–m* crossveins, plus narrow costal band (Fig. 40) . . . . . *Taomyia* Bezzi

67. Wing pattern dark in anterior ½, with small, triangular, hyaline indentation in cell r_1 at apex of pterostigma, hyaline posteriorly with dark transverse band over *dm–m* crossvein to wing margin (Madagascar) . . . . . *Hemilea* Loew

– Wing pattern either largely dark, with hyaline anterior and posterior indentations, or hyaline with dark and partly yellow transverse bands, hyaline indentation in cell r_1 extending at least into cell r_{2+3} (e.g., Figs 35, 38) (continental Afrotropics) 68

68. Wing pattern predominantly brown, with following hyaline areas: oval patch across wing base and bases of cells r_1 and r_{2+3}; two indentations from costal vein (*C*) in apical ½ of cell r_1 to vein R_{4+5}; another

across sub-apical parts of cells r_{2+3} and r_{4+5} to wing margin, near apex of vein M_1; a large rounded marginal patch in cell m_1; an elongate band in cell *cua* alongside vein *CuA+CuP*; and base of discal medial cell (*dm*) (Fig. 38) . . . . . *Ochrobapha* Munro

– Wing pattern hyaline, with partly yellow transverse bands; cell r_1 with broad, hyaline indentation extended at least into discal medial cell (*dm*) (e.g., Fig. 35) 69

69. Head with ocellar setae very short or vestigial; face about as long as frons; antennae > ½ length of face . . . . . *Carpomya* Costa

– Head with ocellar setae well-developed; face distinctly longer than frons; antennae < ½ length of face . . . . . *Myiopardalis* Bezzi

70. Antennae longer than face, with pedicel and postpedicel elongate, subequal in length; 3 pairs of frontal setae and 2 pairs of orbital setae; pterostigma very narrow; discal medial cell (*dm*) very narrow in basal ½, hatchet-shaped (Fig. 68); thorax and abdomen with grey reticulate pattern dorsally (ZACERATINI) . . . . . *Zacerata* Coquillett

– Antennae shorter than face, pedicel much shorter than postpedicel; 2 pairs of frontal setae and 1 pair of orbital setae; pterostigma distinct; discal medial cell (*dm*) not distinctly narrow in basal ½, not hatchet-shaped (e.g., Figs 70–75); thorax and abdomen without grey reticulate pattern (MYOPITINI) 71

71. Mouthparts with labellum long-geniculate, > 0.8 × as long as head length 72

– Mouthparts with labellum spatulate to short-geniculate, < 0.8 × as long as head length 73

72. Abdominal tergites black . . . . . *Asimoneura* Czerny

– Abdominal tergites partly yellow . . . . . *Myopites* Blot

73. Thorax with anepisternum entirely microtrichose . . . . . *Stamnophora* Munro

– Thorax with anepisternum at least partly non-microtrichose, shiny 74

74. Wing with costal setulae along pterostigma enlarged, erect (Fig. 72); scutellum flat, entirely black . . . . . *Spinicosta* Freidberg & Norrbom

– Wing with costal setulae along pterostigma small, not erect (Fig. 74); scutellum convex, yellow medially . . . . . *Urophora* Robineau-Desvoidy

75. Head with posterior orbital setae inclinate, slightly convergent; thorax with anepisternal phragma distinct; dorsocentral and prescutellar acrostichal setae surrounded by distinct black maculae; body and setae largely fulvous (TERELLIINI) . . . . . *Craspedoxantha* Bezzi

– Head with posterior orbital setae reclinate; thorax with anepisternal phragma indistinct, often obscured by dense tomentum; dorsocentral and prescutellar acrostichal setae usually not surrounded by distinct black maculae; body fulvous to black, with setae often black, brown or white 76

76. Antennae longer than face; pterostigma vestigial; wing pattern with narrow, curved, hyaline, sub-apical band from apex of vein R_{2+3} to wing margin in cell m_1, leaving narrow dark costal band; cell *cua* blunt apically; scutellum with 1 pair of marginal setae. . . . . *Pycnella* Munro

– Antennae usually shorter than face; pterostigma sometimes short, but well-developed; wing pattern not as above; cell *cua* often apically acute (e.g., Figs 75, 76, 129); scutellum with 1 or 2 pairs of marginal setae 77

77. Mouthparts with labellum long-geniculate, > 0.8 × as long as head length; head elongate, distinctly longer than high (e.g., Fig. 9); wing pattern blackish or yellow and brown (e.g., Fig. 128); scutellum with 2 pairs of marginal setae, the apicals longer than ½ length of basals (PLIOMELAENINI [in part]) 78

– Mouthparts with labellum not long-geniculate, < 0.8 × as long as head length (e.g., Figs 10–15), if geniculate, then either head not distinctly longer than high (e.g., Fig. 8), or wing pattern greyish and apical scutellar setae not longer than ½ length of basals or absent 80

78. Wing pattern blackish brown, not banded or reticulate, without isolated dark patches on costal vein (C) . . . . . *Euryphalara* Munro

– Wing pattern yellow-brown, banded or reticulate, with dark patches on costal vein (C) 79

79. Wing pattern reticulate; scutellum not black or swollen . . . . . *Deroparia* Munro

– Wing pattern banded (Fig. 128); scutellum black, swollen . . . . . *Xenodorella* Munro

80. Scutellum swollen, polished black; head with 1 pair of orbital setae; outer (lateral) vertical seta longer than orbital seta, black; mouthparts with labellum short; wing pattern banded, with complete hyaline crossband sub-basally and from costal vein (C) in cell r_1 at apex of pterostigma to margin of cell m_1 and

posterior hyaline indentation across cells *bm* and *dm* to margin of cell *cua* (Fig. 76) (CECIDOCHARINI: introduced) . . . . . *Procecidochares* Hendel

– Scutellum usually flat, often yellow, if swollen and black, then head with 2 pairs of orbital setae, the posterior pair often yellow or white; outer (lateral) vertical seta normally shorter than anterior orbital seta, often yellow or white; mouthparts with labellum short (reduced in *Oedaspis*, Fig. 7) or geniculate; wing pattern variable, often not banded. 81

81. Wing vein R_1 without bare, non-setose gap dorsally, posterior to bend at end of subcostal vein (*Sc*), setae evenly spaced (e.g., Figs 75, 77, 78, 107–111, 115, 119, 120, 124–126, 133, 134, 140) 82

– Wing vein R_1 with bare non-setose gap dorsally, posterior to bend at end of subcostal vein (*Sc*) (sometimes with isolated seta medially) (e.g., Figs 97–101, 104, 112–114) 97

82. Mid tibia with erect or suberect setae on anterior surface (AXIOTHAUMINI) 83

– Mid tibia without erect or suberect setae on anterior surface 85

83. Head with 3 pairs of frontal setae; head angular in profile, angle between frons and face *ca* 90° . . . . . *Axiothauma* Munro

– Head with 2 pairs of frontal setae; head oval in profile, angle between frons and face distinctly greater than 90° (e.g., Figs 11, 12) 84

84. Thoracic setae long, curved; wing pattern often M-shaped, well-developed (Fig. 75), although sexes sometimes dimorphic, with pattern reduced in males; male antennal arista unmodified (Fig. 10) . . . . . *Cryptophorellia* Freidberg & Hancock

– Thoracic setae short, straight or virtually straight, nail-like; wing pattern restricted to apical dark macula in male, absent in female; male antennal arista with turbinate plate at apex (Fig. 11) . . . . . *Orthocanthoides* Freidberg

85. Head with 1 pair of orbital setae; wing hyaline, at most with a few indistinct greyish maculae; pterostigma yellow to brown (NOEETINI) . . . . . *Ensina* Robineau-Desvoidy

– Head with 2 pairs of orbital setae; wing almost entirely dark or with distinct dark and hyaline bands or maculae; pterostigma variable in colour (e.g., Figs 79, 108, 110, 111) 86

86. Scutellum swollen, sometimes bilobed; wing pattern with hyaline bands and indentations, bands sometimes reduced to maculae (Figs 78, 79); mouthparts with labellum distinctly reduced (Fig. 7) (DITHRYCINI: PLATENSININA [in part]) . . . . . *Oedaspis* Loew

– Scutellum flat, not distinctly swollen; wing pattern with large, hyaline maculae or almost entirely dark with small hyaline or sub-hyaline maculae (e.g., Figs 108, 110, 111); mouthparts with labellum not distinctly reduced (as in Figs 8–15) 87

87. Wing without isolated and rounded hyaline discal maculae in cells *bm*, r_{4+5} or *dm*; costal cell (*c*) often with dark costal band, but without dark medial macula or transverse band (e.g., Figs 107–111) (TEPHRELLINI [in part]) 88

– Wing usually with hyaline discal maculae, if not, then costal cell (*c*) hyaline, with dark medial macula or transverse band (e.g., Figs 77, 115, 119, 120, 124–126, 133, 134, 140) 91

88. Wing narrow, with marginal hyaline indentation(s) in cell m_1 small, not almost or entirely crossing cell; costal cell (*c*) without dark costal band (e.g., Figs 108, 110, 111) 89

– Wing broad, with marginal hyaline indentation(s) in cell m_1 elongate and almost or entirely crossing cell; costal cell (*c*) usually with dark costal band (e.g., Figs 107, 109) 90

89. Head with 3 pairs of frontal setae and 2 pairs of orbital setae; postocular setae thickened, lanceolate; wing with anal lobe narrow, vestigial (Fig. 108); scutellum with only 1 (basal) pair of marginal setae . . . . . *Dorycricus* Munro

– Head with 1 pair each of frontal and orbital setae; postocular setae thin, sparse; wing with anal lobe large, distinct (Figs 110, 111); scutellum with apical marginal setae present but short . . . . . *Ocnerioxyna* Séguy

90. Head with lunule of moderate size, semicircular . . . . . *Brachyaciura* Bezzi

– Head with lunule large, U-shaped . . . . . *Metasphenisca* Hendel

91. Wing broad, $< 2.5 \times$ as long as wide, with numerous sub-hyaline or silvery discal maculae and narrow hyaline crescent at apices of cells r_{4+5} and m_1 (Fig. 77) (DITHRYCINI: PLATENSININA [in part]) . . . . . *Euthauma* Munro

– Wing not as above, if with numerous sub-hyaline discal maculae, then > 2.5 × as long as wide; if pattern with hyaline macula at apex of cell r_{4+5}, then not extendlng into cell m_1 (e.g., Figs 115, 119, 120, 124–126, 133, 134, 140) (PLIOMELAENINI & TEPHRITINI [both in part]) 92

92. Wing pattern grid-like, with large, subrectangular, partly confluent hyaline maculae separating 3 dark brown areas: 1) at pterostigma, 2) from apex of vein R_{2+3} through crossvein *dm–m* and 3) at apex; pterostigma with pale yellowish patch (Fig. 140) . . . . . *Ptosanthus* Munro

– Wing pattern not as above, widely dark with smaller round isolated yellowish, pale brown or hyaline maculae; pterostigma with or without pale patch (e.g., Figs 115, 119, 120, 124–126, 133, 134). . . . 93

93. Wing narrow, *ca* 3.0 × as long as wide, with numerous pale brown, or yellowish discal maculae, hyaline marginal indentations in cell r_1 not crossing vein R_{2+3} and 2 marginal hyaline indentations in cell m_1 (Fig. 115). . . . . *Elaphromyia* Bezzi

– Wing broader, *ca* 2.0–2.5 × as long as wide; wing pattern not as above (e.g., Figs 119, 120, 124–126, 133, 134). 94

94. Wing with discal medial cell (*dm*) largely yellow and brown, cell r_{4+5} with large, hyaline macula filling entire apex (Fig. 126). . . . . *Pterope* Munro

– Wing with discal medial cell (*dm*) largely brown, if with yellowish sub-hyaline maculae, then apical macula in cell r_{4+5} very small or absent (Note: two undescribed genera from Kenya (Fig. 129) and Cameroon (Fig. 130), also key here; they are best identified by reference to the figures before proceding with the key) 95

95. Wing pattern grey and pale yellow in males, brownish black in females; apex of cell r_{4+5} entirely dark; cell m_1 with 3 large hyaline marginal maculae, basal macula separated from large anterior macula adjacent to middle of crossvein *dm–m* in males, united into elongate macula in females (Figs 133, 134); scutellum with apical marginal setae < ½ length of basal marginal setae . . . . . *Chipingomyia* Hancock

– Wing pattern not as above in males, but often with pale or yellow areas anteriorly; apex of cell r_{4+5} often with hyaline macula; cell m_1 with 1–4 small, rounded marginal maculae and at most small basal macula well distant from crossvein *dm–m*; scutellum with apical marginal setae at least ⅔ length of basal marginal setae (e.g., Figs 119, 120, 124, 125). 96

96. Wing with distinct hyaline or yellowish maculae in at least apical ⅔ of anal lobe (Figs 119, 120) . . . . . *Manicomyia* Hancock

– Wing with anal lobe dark, without distinct hyaline maculae in apical ⅔ (Figs 124, 125) . . . . . *Pseudafreutreta* Hering

97. Body generally shiny black, with fine pubescence on scutum (coarse in *Oedoncus*) and abdomen, sometimes reddish or with bronzy sheen; thorax with postpronotal lobe shiny black or red, not contrasting with rest of scutum; head often with postocular setae entirely thin, black; wing without either bullae or dark transverse medial band or macula in costal cell (*c*) (e.g., Figs 94–106, 112, 113) (TEPHRELLINI [in part]) 98

– Body generally fulvous to black, with coarse pubescence on scutum and abdomen; thorax with postpronotal lobe yellow to dark brown, usually contrasting with rest of scutum, if shiny black, then wing with distinct bullae; head usually with at least some postocular setae thick and white; wing often with dark transverse medial band or macula in costal cell (*c*) (e.g., Figs 80, 117–120, 122–124, 127–141, 143, 150, 162, 169, 171, 173) 112

98. Scutellum with 2 pairs of marginal setae. 99

– Scutellum with 1 pair of marginal setae 101

99. Wing pattern not banded, with either 1 broad (sometimes diffusely yellow), or 2 triangular hyaline indentations on anterior margin distal to pterostigma (Figs 97–101). . . . . *Dicheniotes* Munro

– Wing pattern banded, with single hyaline crossband or triangular indentation on anterior margin distal to pterostigma (e.g., Fig. 104). 100

100. Scutellum swollen; mouthparts with labellum geniculate, > 0.55 × as long as head (Fig. 8); wing with complete, hyaline, crossband from costal vein (*C*) at apex of vein R_1 to hind margin; *r–m* and *dm–m* crossveins closely approximated (Fig. 104) . . . . . *Oedoncus* Speiser

– Scutellum not swollen; mouthparts with labellum short, not geniculate, < 0.55 × as long as head; wing with triangular, hyaline indentation from costal vein (*C*) at apex of vein R_1; *r–m* and *dm–m* crossveins well-separated . . . . . *Sphaeniscus* Becker

101. Head with 2 pairs of orbital setae. 102

– Head with 1 pair of orbital setae 106

102. Wing with either alula or anal lobe usually distinctly narrowed, cell *cua* narrow, blunt apically (e.g., Figs 112–114). 103

– Wing with alula and anal lobe normal, cell *cua* broad, acute apically (e.g., Fig. 102). 105

103. Wing broad, < 2.7 × as long as wide, with 2 posterior hyaline indentations in cell m_4 elongate, with at least the basal indentation extending into discal medial cell (*dm*) (Fig. 112) . . . . . *Tephraciura* Hering

– Wing narrow, > 2.7 × as long as wide, with 2 posterior hyaline indentations in cell m_4 short and broad, not extending into discal medial cell (*dm*) (e.g., Figs 113, 114) 104

104. Wing base black, with hyaline crossband; calypters white; head with 2 pairs of frontal setae (restricted to Madagascar) . . . . . *Malagaciura* Hancock

– Wing base mostly hyaline (Figs 113, 114); calypters black; head with 3 pairs of frontal setae (not restricted to Madagascar) . . . . . *Paraciura* Hering

105. Wing with 3 posterior hyaline indentations, the apex broadly black . . . . . *Aciura* Robineau-Desvoidy

– Wing with 4 posterior hyaline indentations; leaving distinct apical band aligned with costal vein (Fig. 102). . . . . *Gymnaciura* Hering

106. Head with lunule large, U-shaped, 0.3 × as long as frons; wing with argents (*i.e.*, silvery maculae) (Fig. 106). . . . . *Ypsilomena* Munro

– Head with lunule of moderate size, semicircular, < 0.25 × as long as frons; wing with or without argents (e.g., Figs 94–96, 103, 105). 107

107. Wing with *r–m* and *dm–m* crossveins closely approximated, with 4 isolated and narrow dark crossbands (Fig. 95) . . . . . *Munroella* Bezzi

– Wing with *r–m* and *dm–m* crossveins well-separated, without isolated dark crossbands (e.g., Figs 94, 96, 103, 105). 108

108. Wing pattern widely dark anteriorly, hyaline posteriorly, without hyaline marginal indentations (Fig. 103). . . . . *Katonaia* Munro

– Wing with hyaline indentations anteriorly and posteriorly (e.g., Figs 94, 96, 105) 109

109. Wing pattern banded, with black basal patch and 1 hyaline indentation beyond pterostigma (not yet recorded from the Afrotropics) . . . . . [*Paraspheniscus* Hendel]

– Wing pattern not banded, if so, then base hyaline and/or 2 hyaline indentations beyond pterostigma (e.g., Figs 105) 110

110. Wing with argents (silvery maculae) and black costal band at base separated from discal dark area by hyaline band; hyaline indentations beyond pterostigma triangular, both extending beyond vein R_{4+5} (Fig. 105) . . . . . *Oxyaciura* Hendel

– Wing without argents and base entirely hyaline; hyaline indentations beyond pterostigma not triangular, either both not extending beyond vein R_{4+5} or both reaching hind margin of wing as complete bands (e.g., Figs 94, 96) 111

111. Head with pale postocular setae; scutum distinctly tomentose . . . . . *Afraciura* Hering

– Head with black postocular setae; scutum shiny black . . . . . *Paraspheniscoides* Hering

112. Head with black macula on parafacial near antennal base (e.g., Figs 13–15); if not, then wing with both costal cleft at base of pterostigma and shiny bullae darker than surrounding pattern; or dorsal surface of scutellum with 1 or more pairs of erect or suberect discal whitish setulae; or ventral margin of head sloping downwards, so that area below eye level wider posteriorly than anteriorly and wing pattern extensively black in anteroapical ⅔ and without numerous discal maculae or reticulation (e.g., Figs 80–93, 116, 121) (PLIOMELAENINI, EUTRETINI & SCHISTOPTERINI [all in part]) 113

– Head without black macula on parafacial near antennal base, with ventral margin horizontal; wing without both costal cleft and bullae darker than surrounding pattern; pattern often distinctly maculate, reticulate or largely hyaline (e.g., Figs 117, 118, 122, 123, 127, 131, 132, 135–139, 141–143, 145–161, 163–169, 172, 173, 175); scutellum without erect or suberect whitish discal setulae on dorsal surface (PLIOMELAENINI & TEPHRITINI [both in part]) 131

113. Wing very wide oval, < 2 × as long as wide, pattern mostly dark with numerous short anterior and posterior hyaline indentations; no large maculae or reticulation in discal medial cell (*dm*); small discal maculae in anterior ½ and black bullae (Fig. 80); head with anterior orbital setae on, or in front of, line of posterior frontal setae; parafacial with black macula (EUTRETINI [in part]) . . . . . *Perirhithrum* Bezzi

– Wing distinctly longer than broad, not almost circular in shape, pattern variable, often densely hyaline maculate or reticulate in discal medial cell (*dm*) and with, or without, black bullae (e.g., Figs 81–93, 116, 121); anterior orbital setae inserted well behind posterior frontal setae; parafacial with or without black macula 114

114. Wing pattern dark, without shiny black bullae, although often with darker black discal patches, with or without very short anterior and posterior hyaline indentations and numerous sub-hyaline maculae over disc; wing apex usually with distinct hyaline crescent over entire cell r_{4+5} and anterior corner of cell m_1 (e.g., Figs 116, 121); head with parafacial with black macula (PLIOMELAENINI [in part]) 115

– Wing pattern variable, often densely hyaline maculate or reticulate in discal medial cell (*dm*) (e.g., Figs 81–93), with or without black bullae; head with or without parafacial black macula. 116

115. Wing pattern with very short anterior and posterior hyaline indentations and numerous sub-hyaline maculae over disc (Fig. 116). . . . . *Ghentia* Munro

– Wing pattern without anterior and posterior hyaline indentations (Fig. 121) . . . . . *Platomma* Bezzi

116. Scutellum with marginal setae, but without 1 or more pairs of erect, or suberect, whitish discal setulae on dorsal surface; wing without costal cleft at base of pterostigma; without shiny bullae darker than surrounding pattern, but often with silvery argents (e.g., Fig. 81) (EUTRETINI [in part]) 117

– Scutellum usually with 1 or more pairs of erect, or suberect, discal whitish setulae on dorsal surface in addition to marginal setae, if not, then wing with distinct costal cleft at base of pterostigma; with shiny bullae darker than surrounding pattern (e.g., Figs 82–93) (SCHISTOPTERINI [in part]) 119

117. Head with mesofrons bare, or only very slightly setose anteriorly; ventral margin of head sloping downwards (Fig. 13), so that area below eye level wider posteriorly than anteriorly (Fig. 13); facial maculae present or wing largely hyaline in posterior ½; thorax with dorsocentral setae closer to line of supra-alar setae than to transverse suture; ventral calypter distinctly narrower than dorsal calypter . . . . . .*Afreutreta* Bezzi

– Head with mesofrons densely setose; ventral margin of head horizontal (e.g., Figs 14, 15); facial maculae present; thorax with dorsocentral setae closer to transverse suture than to line of supra-alar setae; ventral calypter as wide as, or wider than, dorsal calypter 118

118. Wing without small, hyaline maculae over entire surface, but with large pale central patch and numerous argents; abdominal setulae brownish . . . . . *Cosmetothrix* Munro

– Wing with numerous small, hyaline maculae over entire surface and argents superimposed on them (Fig. 81); abdominal setulae whitish in posterior ½ of tergites. . . . . *Tarchonanthea* Freidberg & Kaplan

119. With the following combination of characters (or at least most of them: 6 of 8): head without postocellar setae (except in *Brachiopterna ornithomorpha* (Munro, 1931)); 1 pair of lateral postocellar or paravertical setae; with distinct facial carina; without whitish, erect setae or setulae on scutellum; body mostly black, with shiny and microtrichose parts; legs mostly black, although tibiae and tarsi usually at least partly yellow; wing pattern *Schistopterum*-type, mostly brown to black, usually with only few small round hyaline maculae (fewer than 10) (e.g., Figs 82–84); host-plants Plucheae 120

– With the following combination of characters (or at least most of them: 6 of 8): interfrontal setae almost invariably present, even if setula-like) *ca* 0.25 × as long as ocellar setae); at least 2 pairs of postocellar setae; with facial carina indistinct (except distinct in *Rhabdochaeta*); body mostly greyish, brownish, yellowish or whitish, rarely blackish, usually extensively microtrichose; legs often predominantly or entirely yellow; wing pattern mostly grey to brown, usually with numerous (10–100) small- to medium-sized, round, hyaline maculae (e.g., Figs 85–93); host-plants non-Plucheae (several undescribed genera are known) 122

120. Head with 2 pairs of orbital setae; 3 pairs of frontal setae, the anterior pair whitish, lanceolate, middle and posterior pairs brownish black, acuminate; antennal postpedicel short, 1.65–2.40 × as long as high, strongly arched ventrally, strongly narrowed towards slightly rounded apex; wing with dark ray extending from centre of pattern to costal vein (C) between veins R_1 and R_{2+3} (Fig. 83). . . . . *Brachiopterna* Bezzi

– Head with 1 pair of orbital setae; 1 or 2 pairs of frontal setae, all brownish black, acuminate; antennal postpedicel long, 2.5–7.0 × as long as high, parallel-sided, apex slightly rounded or truncate; wing without dark ray as described above (e.g., Figs 82, 84) 121

121. Head with all postocular setae black, acuminate; thorax with whitish setulae on scutum, arranged in 3 distinct longitudinal vittae: 1 median and 2 lateral; wing with pterostigma at least 3 or 4 × as long as wide, but less than ½ length of costal cell (c) (Fig. 82). . . . . *Bactropota* Bezzi

– Head with 1 or all postocular setae whitish; thorax with whitish setulae on scutum, arranged either more or less uniformly, or in 5 longitudinal vittae, with 1, 3 and 5 wider than 2 and 4; wing with pterostigma reduced, 1 or 2 × as long as wide, much shorter than costal cell (*c*) (Fig. 84). . . . . *Schistopterum* Becker

122. Head with 2 pairs of interfrontal setae; antennal pedicel with long, ventral, whitish seta almost as long as postpedicel; wing pattern with fine, transverse white lines within dark discal area (Fig. 93). . . . . *Setoides* Zonstein & Freidberg

– Head with at most 1 pair of interfrontal setae; antennal pedicel without long, ventral, whitish seta; wing pattern without fine, transverse white lines within dark discal area [Note: an undescribed genus from Madagascar differs from the remaining genera, in having truncate wing apex, straight between apices of veins R_{4+5} and M_1; a second undescribed genus from Nigeria to Kenya differs from remaining genera in having wing pattern comprised of large, dark central area and 6–8 grey, wide, ill-defined branches extending from centre of cell r_1 to vein M_1 with most branches from pterostigma to vein R_{4+5} filled with hyaline maculae] 123

123. Wing relatively broad, *ca* 2 × as long as wide; pattern with numerous hyaline maculae over disc, but not distinctly rayed or reticulate, except apically in an undescribed Madagascan *Eutretosoma* species; wing apex hyaline or with reticulation usually fainter than remaining pattern; costal cleft shallow (e.g., Figs 87, 89); head with very short ocellar setae; body colour brown or black [Note: an undescribed genus from Kenya, Nigeria and Tanzania has the costal cleft *ca* ½ width of pterostigma, ocellar setae long and palpus long and protuberant] 124

– Wing relatively narrow, usually > 2 × as long as wide; pattern distinctly rayed or reticulate; wing apex rayed or with reticulation often darker than remaining pattern (e.g., Figs 85, 86, 88, 90–92); ocellar setae, costal cleft and body colour variable 125

124. Antennae *ca* as long as face, antennal postpedicel rounded or attenuated into dorsoapical point, but not parallel-sided; head with face (in lateral view) evenly and smoothly concave, without distinct dorsal bulge or transverse furrow, but with ventral margin distinctly protuberant; wing pattern faint at apex, bullae large and distinct (Fig. 87) . . . . . *Eutretosoma* Hendel

– Antennae distinctly longer than face, generally parallel-sided; head with face in lateral view variable, but not evenly and smoothly concave, usually with distinct transverse furrow; wing pattern narrowly hyaline at apex, bullae small and indistinct (Fig. 89) . . . . . *Microtreta* Freidberg

125. Head with posterior pair of frontal setae strongly lanceolate, distinctly wider than any other setae; scutum and sometimes abdomen with erect, whitish setae; apex of abdomen with shiny and usually black area, strongly contrasted with remaining paler matt areas; antennal postpedicel usually attenuated, pointed; facial carina large or indistinct 126

– Head with posterior pair of frontal setae acuminate, not distinctly wider than adjacent frontal setae; scutum and abdomen without erect setae; apex of abdomen black, shiny or microtrichose (as remaining parts of abdomen), but not strongly contrasted with remaining black areas of abdomen; antennal postpedicel variable; facial carina indistinct or absent 127

126. Abdomen without double row of erect yellowish setae; head with face in dorsal ½ with conspicuous large carina, ventral ½ strongly protuberant; antennal postpedicel elongate, *ca* 2 × as long as face height, tapered gradually; wing wide, *ca* 2.2 × as long as wide; wing with dark rays to wing margin, usually with hyaline filling, at least in cell r_1, white rays between dark rays usually present (Fig. 90) . . . . . *Rhabdochaeta* de Meijere

– Abdomen dorsomedially with double row of erect yellowish setae; head with face in dorsal ½ with indistinct carina, ventral ½ slightly protuberant; antennal postpedicel only slightly longer than face height, apex produced into elongate projection; wing *ca* 2.5 × as long as wide; wing with dark rays to margin usually without hyaline filling, without white rays between dark rays (Fig. 91) . . . . . *Rhochmopterum* Speiser

127. Wing pattern distinctly rayed, with 3–8 bullae in large, dark discal area; costal cleft deep (except in some *Melanopterella*) (e.g., Figs 85, 88); head with distinct interfrontal setae, usually 0.8–0.9 length of ocellar setae [Note: interfrontal setae short or absent in *Tanzanimyia* Freidberg, Zonstein & Friedman (Freidberg *et al*. 2020)]. 128

– Wing pattern pale, reticulate, not distinctly rayed, with 0–2 bullae in (at most) small and rounded dark discal area; costal cleft shallow (e.g., Figs 85, 92); head with interfrontal setae short or absent 129

128. Body generally stout; paler species, with body and wing pattern predominantly brownish, yellowish or whitish; wing with costal cleft conspicuous, extending to *ca* mid width of pterostigma; head with ocellar

and interfrontal setae subequal, *ca* as long as antennal postpedicel; palpus large, protuberant; wing pattern extensive and with 6–8 bullae (Fig. 85) . . . . . *Cordylopteryx* Hering

– Body usually slender; body and wing pattern usually dark (black or blackish); if pale, then usually greyish; wing with costal cleft usually shallower, often barely distinct; head with ocellar and interfrontal setae usually shorter than antennal postpedicel; interfrontal setae usually as long as, or slightly longer than, ocellar setae; palpus usually not protuberant; wing pattern extensive or reduced, apex with 4 more or less similar, narrow, discrete rays, usually with fewer than 6 bullae (Fig. 88). . . . . *Melanopterella* Freidberg

129. Wing pattern without dark discal patch or bullae, uniformly greyish, evenly reticulate, with moderately large, round hyaline maculae, except darker apex of wing and sometimes along distal sections of veins R_{4+5} and M_1 (Fig. 92); head without interfrontal setae; female oviscape considerably longer than remainder of abdomen, basally conical, distally cylindrical . . . . . *Schistotephritis* Freidberg

– Wing pattern with darker discal patch and 1 or 2 small bullae, not distinctly darker at apex; head usually with interfrontal setae; female oviscape usually considerably shorter than remainder of abdomen, differently shaped, more or less flattened dorsoventrally. 130

130. Head with ocellar seta *ca* as long as antennal postpedicel, interfrontal seta considerably shorter, barely distinct or absent; wing with greyish, brownish or blackish pattern; blackish bulla variable, from small and squarish to large and quadrangular; female postabdomen with oviscape at least as long as tergites 5 and 6 (Fig. 85) . . . . . *Clematochaeta* Hering

– Head with ocellar and interfrontal setae subequal, distinctly shorter than antennal postpedicel; wing with yellowish or pale brownish pattern; blackish bulla small, squarish; female postabdomen with oviscape *ca* as long as tergite 6 . . . . . *Heringomyia* Hardy

131. Antenna elongate, narrow, parallel-sided, longer than face; pedicel almost as long as postpedicel; wing with last section of costal vein (C), in cell r_{4+5}, hyaline, inconspicuous but not reduced (Fig. 118) . . . . . *Leucothrix* Munro

– Antenna moderately wide, shorter than face; pedicel much shorter than postpedicel; wing with last section of costal vein (C), in cell r_{4+5}, either brown or reduced (e.g., Figs 117, 122, 123, 127, 131, 132, 135–139, 141–143, 145–161, 163–176) 132

132. Costal wing vein (C) ending at vein R_{4+5}, pattern usually grid-like, not banded; if banded, then 2 longest bands parallel (Fig. 127) (*Hyaloctoides superhyalinus* (Munro, 1929) also runs here, but differs in having 2 hyaline indentations in cell r_1 parallel, outer indentation broad and shorter than its own width from apex of cell) . . . . . *Triandomelaena* Hancock

– Costal wing vein (C) ending at vein M_1, if reduced, then pattern banded with 2 longest bands convergent posteriorly or (some *Hyaloctoides*) as noted above (e.g., Figs 117, 122, 123, 131, 132, 135–139, 141–143, 145–161, 163–176) 133

133. Wing with apical sections of veins R_{4+5} and M_1 divergent; wing pattern with 2 hyaline indentations in cell r_1 parallel, second extending into cell r_{2+3}; 0–1 hyaline marginal indentation in cell r_{2+3} below apex of vein R_{2+3}; apical hyaline macula elongate, crossing entire apex of cell r_{4+5}; hyaline discal maculae and indentations often enlarged (Fig. 117); scutellum with apical marginal setae 0.8 × as long as basal marginal setae . . . . . *Hyaloctoides* Munro

– Wing with apical sections of veins R_{4+5} and M_1 more or less parallel (except in *Brachydesis*); wing membrane pattern variable, but not as above (e.g., Figs 122, 123, 131, 132, 135–139, 141–143, 145–161, 163–176); scutellum with apical marginal setae often much shorter than basal marginal setae or absent 134

134. Wing pattern dark, with hyaline indentations and discal maculae, 2 basal indentations in cell r_1 and associated macula in cell r_{2+3} arranged into V-shaped pattern; cell r_{2+3} with single, small, hyaline marginal macula below apex of vein R_{2+3}; apex of cell r_{4+5} with hyaline macula not completely crossing cell (e.g., Figs 122, 123); scutum with fine, pale microtrichia; abdomen shiny black or reddish, without coarse pale microtrichia; scutellum with apical marginal setae at least ½ length of basal setae 135

– Wing pattern not as above (e.g., Figs 131, 132, 135–139, 141–143, 145–161, 163–176); scutum and abdomen often with coarse pale microtrichia; scutellum with apical marginal setae often much shorter than basal setae or absent 136

135. Head with lateral part of subcranial cavity with strong, bristle-like setae, *ca* 0.5–0.75 length of genal seta . . . . . *Pliomelaena* Bezzi

– Head with lateral part of subcranial cavity with row of fine, moderately strong, but not bristle-like, setae . . . . . *Psednometopum* Munro

136. Abdominal tergites largely or entirely shiny black, with fine pubescence; scutellum usually with 1 pair of marginal setae, the apical setae (if present) < ½ length of basal setae (*Spathulina*-group) 137
– Abdominal tergites usually densely or coarsely pubescent, at most partly shiny black; scutellum usually with 1 or 2 pairs of marginal setae 143
137. Wing hyaline or slightly infuscated on disc, but without distinct pattern; usually large hyaline patch at apex of cell r_{4+5} (e.g., Figs 145, 147). 138
– Wing membrane largely dark with hyaline bands, discal maculae and indentations (e.g., Figs 146, 148–152). 139
138. Palpus mostly or entirely yellow; head with 1 or 2 pairs of orbital setae; wing cells *bc* and *c* hyaline or lightly infuscated (Fig. 145); halter yellow. . . . . *Elgonina* Munro
– Palpus black; head with 1 pair of orbital setae; wing cells *bc* and *c* black (Fig. 147); halter black . . . . . *Marriottella* Munro
139. Wing base black, disc with elongate hyaline indentation across cells r_1 and r_{2+3} from apex of pterostigma; subapical band complete across cells r_{2+3} and r_{4+5}; with 2 transverse indentations across cells r_{4+5} and m_1 and an oblique band across cells *br* and *dm* (Fig. 149) . . . . . *Peratomixis* Munro
– Wing base mostly hyaline, disc with numerous hyaline indentations and maculae (e.g., Figs 146, 148, 150–152). 140
140. Wing pattern with 3 subrectangular maculae crossing cell r_1 from costal vein (*C*) and single large macula in cell r_{2+3}, posterior of apex of vein R_{2+3}; wing apex with large hyaline macula isolated from that in cell r_{2+3} (Fig. 146). . . . . *Gymnosagena* Munro
– Wing pattern with 1 or 2 large indentations crossing cell r_1 from costal vein (*C*) and often a third small macula near apex of cell and 1 or 2 marginal indentations in cell r_{2+3}, posterior to apex of vein R_{2+3} often small or absent; wing apex with large hyaline macula sometimes confluent with marginal macula in cell r_{2+3} (e.g., Figs 148, 150–152) 141
141. Wing pattern with 2 quadrate hyaline indentations in cell r_1 often coalescing into one; if not, then cell m_4 largely hyaline in basal ½; anal lobe hyaline (Fig. 148); abdominal tergites often yellow posteriorly . . . . . *Migmella* Munro
– Wing pattern with hyaline indentations in cell r_1 widely separated, if partly fused, then cell m_4 almost entirely dark in basal ½; anal lobe often largely dark (e.g., Figs 150–152); abdominal tergites entirely black 142
142. Scutellum with 1 pair of marginal setae, without apical setae . . . . . *Spathulina* Rondani
– Scutellum with 2 pairs of marginal setae, apical setae ½ length of basal setae . . . . *Tephritoresta* Hering
143. Scutellum with apical marginal setae well-developed, *ca* as long as basal setae; thorax with posterior notopleural seta black or brown; anepimeral seta brown; wing pattern normally reticulate with darker transverse band across both *r–m* and *dm–m* crossveins and darker apex, but without apical fork (e.g., Figs 154–159); sometimes pattern reduced; if apex mostly hyaline, then pterostigma with hyaline macula; if wing sub-hyaline, without distinct pattern (e.g., Fig. 153), then antennal postpedicel with distinct apical point (*Sphenella* group) 144
– Scutellum with apical marginal setae often much shorter than basal setae or absent; thorax with posterior notopleural seta white or yellow, if black and apical scutellar setae well-developed, then anepimeral seta white; wing pattern variable, but often with apical fork (e.g., Figs 131, 132, 135–139, 141–143, 160, 161, 163–169, 172, 173, 175, 176, 274); if wing hyaline or sub-hyaline without distinct pattern, then antennal postpedicel without apical point 149
144. Wing sub-hyaline, without distinct pattern (Fig. 153); antennal postpedicel with distinct apical point. . . . . *Acronneus* Munro
– Wing with distinct pattern (e.g., Figs 154–159); antennal postpedicel apically rounded 145
145. Wing vein R_{4+5} setose to *r–m* crossvein or beyond (e.g., Figs 155–157, 159) 146
– Wing vein R_{4+5} bare or with 1–3 setulae at node (e.g., Figs 154, 158) 148
146. Thorax with anepimeral seta red-brown; wing pattern with reticulation dark, apical dark area often indistinct (Figs 155, 156) . . . . . *Parafreutreta* Munro
– Thorax with anepimeral seta pale brown; wing pattern with reticulation pale, often indistinct, apical area broad and distinctly darker (e.g., Figs 157, 159) 147
147. Hind femur with anteroventral row of setae *ca* as long as width of femur . . . . . *Paratephritis* Shiraki

– Hind femur without anteroventral row of setae *ca* as long as width of femur . . . . . *Telaletes* Munro

148. Scutellum swollen, black, if only slightly convex and brownish, then wing with elongate, hyaline indentation in apical dark area with subapical portion broad, ending at hind wing margin; dark median band very broad over crossvein *dm–m* (Fig. 154) (includes *Bevismyia* Munro) . . . . . *Oedosphenella* Frey

– Scutellum flat, yellowish or yellowish brown, if wing with hyaline indentation in apical dark area, then subapical portion narrow, ending well before hind wing margin; pattern sometimes with dark median band very narrow or reduced to maculae over crossvein *dm–m* (Fig. 158) . . . . . *Sphenella* Robineau-Desvoidy

149. Wing with large, isolated, dark brown subbasal macula across cells *br* and *bm*; apical ⅔ dark brown, with darker subapical patch and very large, hyaline maculae, including single marginal one in cell r_{2+3} below apex of vein R_{2+3} (Fig. 143) (*Euaresta*-group) . . . . . *Euaresta* Loew

– Wing without large, isolated, dark brown subbasal macula across cells *br* and *bm* and pattern variable, often with 2 marginal maculae in cell r_{2+3} below apex of vein R_{2+3} (e.g., Figs 131, 132, 135–139, 141, 142, 160, 161, 163–176). 150

150. Wing without pattern or with single hyaline marginal indentation in cell r_{2+3} below apex of vein R_{2+3}, if 2 hyaline indentations, then posterior one smaller, isolated (e.g., Figs 131, 132, 135–139, 141, 142); if wing hyaline, then mouthparts with labellum geniculate (PLIOMELAENINI [in part] and *Campiglossa* group) 151

– Wing pattern with 2 hyaline marginal indentations in cell r_{2+3} below apex of vein R_{2+3}, posterior macula larger, often united with other maculae (e.g., Figs 160, 161, 163–169, 172–176); if wing hyaline or virtually so, then mouthparts with labellum not geniculate (*Tephritis* group) 163

151. Wing hyaline, with yellowish pterostigma or with faint reticulation (Fig. 142); mouthparts with labellum geniculate; femora black at least over basal $^{7}/_{10}$; thorax with posterior notopleural seta black . . . . . *Tanaica* Munro

– Wing pattern distinct (e.g., Figs 131, 132, 135–139, 141); mouthparts with labellum geniculate or not; femora usually not as above; thorax with posterior notopleural seta black or white. 152

152. Wing hyaline with dark bands or maculae, pattern not mostly dark or reticulate; subbasal band and band across *dm–m* crossvein convergent posteriorly; costal vein (C) ending at either vein R_{4+5} or M_1; mouthparts with labellum short, capitate . . . . . *Stephanotrypeta* Hendel

– Wing pattern not as above; if banded, then bands not convergent posteriorly and mouthparts with labellum geniculate; costal vein (C) ending at vein M_1 (e.g., Figs 131, 132, 135–139, 141) 153

153. Wing pattern mostly dark, without hyaline indentation in cell r_{2+3}, adjacent to apex of vein R_{2+3} (e.g., Fig. 132) 154

– Wing pattern variable, but with hyaline indentation in cell r_{2+3}, adjacent to apex of vein R_{2+3} (e.g., Figs 131, 135–139, 141). 155

154. Wing base hyaline; pterostigma distinctly paler basally; cell m_4 with 3 hyaline indentations (Fig. 132) . . . . . *Bezzina* Munro

– Wing base dark; pterostigma entirely black; cell m_4 with 2 hyaline indentations . . . . *Pediapelta* Munro

155. Wing distinctly elongate, > 2.7 × as long as broad . . . . . *Namwambina* Munro

– Wing not distinctly elongate, < 2.7 × as long as broad (e.g., Figs 131, 135–139, 141) 156

156. Wing pattern largely dark, with numerous hyaline maculae and indentations, the 3 large maculae in cell r_1 and middle of cell r_{2+3} forming distinct V-shaped group; cell r_{4+5} without hyaline apical macula (Fig. 138). . . . . *Mastigolina* Munro

– Wing pattern not as above, often reticulate or reticulate/banded; cell r_{4+5} often with hyaline apical macula (e.g., Figs 131, 135–137, 139, 141) 157

157. Scutellum with 1 pair of marginal setae, without apical setae; head with 2 pairs of frontal setae . . . 158

– Scutellum with 2 pairs of marginal setae; head with 1–3 pairs of frontal setae 159

158. Head elongate; frons 1.5 × as long as wide; parafacial wide; abdomen with distinct maculae . . . . . *Dioxyna* Frey

– Head not elongate; frons *ca* as long as wide; parafacial narrow; abdomen without distinct maculae. . . . . *Lethyna* Munro

159. Head with 1 pair of frontal setae; scutellum with long apical marginal setae . . . . . *Antoxya* Munro

– Head with 2 pairs of frontal setae; scutellum with long or short apical marginal setae 160

160. Scutellum with apical marginal setae at least 0.75 length of basal marginal setae; thorax with posterior notopleural setae black 161
– Scutellum with apical marginal setae at most 0.6 length of basal marginal setae; thorax with posterior notopleural setae black or white 162
161. Head with parafacial wide; mouthparts with labellum geniculate, longer than mouth opening; wing with basal costal cell (*bc*) dark and pattern often dimidiate; pterostigma dark basally, often with hyaline macula apically (Fig. 139) . . . . . *Mesoclanis* Munro
– Head with parafacial narrow; mouthparts with labellum capitate, *ca* ½ length of mouth opening; wing with basal costal cell (*bc*) hyaline and pattern not dimidiate; pterostigma dark apically, often pale basally (Fig. 141) . . . . . *Scedella* Munro
162. Wing pattern reticulate, subreticulate or reduced; pterostigma with or without hyaline macula (Fig. 135); mouthparts with labellum not long-geniculate, at most only slightly longer than mouth opening . . . . . *Campiglossa* Rondani
– Wing pattern usually banded or barred; pterostigma usually without hyaline macula (Fig. 136); mouthparts with labellum long-geniculate, much longer than mouth opening . . . . . *Desmella* Munro
163. Wing with pterostigma very short, *ca* as long as wide (e.g., Figs 160–162); lower calypter very narrow, strip-like; scutellum with 1 pair of marginal setae 164
– Wing with pterostigma at least 2 × as long as wide (e.g., Figs 163–169, 172–176); lower calypter variable; scutellum with 1 or 2 pairs of marginal setae 166
164. Head with 1 pair of orbital setae . . . . . *Actinoptera* Rondani
– Head with 2 pairs of orbital setae, posterior pair shorter. 165
165. Head with 3 pairs of frontal setae, anterior pair white; mouthparts with labellum geniculate . . . . . *Brachydesis* Hancock
– Head with 2 pairs of dark frontal setae; mouthparts with labellum capitate or slightly spatulate . . . . . *Brachytrupanea* Hancock
166. Head with medial postocellar setae (pair of short setae between postocellar setae, directly posterior to ocelli (see Merz 1999: 652, figs 24.6A & 6C)); all postocular setae white 167
– Head without medial postocellar setae; postocular setae variable. 171
167. Scutellum with 1 pair of marginal setae 168
– Scutellum with 2 pairs of marginal setae. 169
168. Thorax with dorsocentral setae inserted well behind transverse suture; wing with discal medial cell (*dm*) usually crossed by at least 1 complete broad dark ray. . . . . *Euarestella* Hendel
– Thorax with dorsocentral setae inserted almost in line of transverse suture; wing with discal medial cell (*dm*) at most with narrow, incomplete transverse dark ray (Figs 165, 166). . . . . *Goniurellia* Hendel
169. Wing pattern strongly reduced, faint, sometimes lacking (Fig. 167); head without frontal vitta . . . . . *Hyalotephritis* Freidberg
– Wing pattern more extensive, with at least 1 entire hyaline macula (e.g., Figs 163, 164, 168, 169, 172–176); head with frontal vitta, but sometimes weakly developed 170
170. Head with ocellar triangle without setulae; wing pattern reticulate or elongate/stellate, with bulla (Fig. 168). . . . . *Insizwa* Munro
– Head with ocellar triangle with whitish setulae; wing pattern narrow/stellate, without bulla (Fig. 172) . . . . . *Stelladesis* Merz
171. Head with all postocular setae whitish 172
– Head with at least some short postocular setae black 181
172. Scutellum with 1 pair of marginal setae . . . . . *Trupanea* Schrank
– Scutellum with 2 pairs of marginal setae. 173
173. Head with 1 pair of black orbital setae; thorax with posterior notopleural seta black; dorsocentral setae almost at level of supra-alar setae; wing entirely hyaline. . . . . *Arabodesis* Merz & Dawah
– Head with 2 pairs of orbital setae; thorax with posterior notopleural seta white; dorsocentral setae closer to suture than to supra-alar setae; wing usually with distinct, although sometimes weak, pattern (e.g., Figs 173, 175) 174

174. Head with 2 pairs of dark frontal setae 175
– Head with 3 pairs of frontal setae, the anterior pair sometimes white 176
175. Lower calypter with convex outer margin . . . . . *Tephritis* Latreille
– Lower calypter very narrow, strap-like, with straight outer margin . . . . . *Tephrodesis* Merz [in part]
176. Head with 3 pairs of frontal setae, anterior pair white; mouthparts short-spatulate or geniculate; wing pattern elongate/stellate, stellate pattern connected to pterostigma by broad brown ray . . . . . *Capitites* Foote & Freidberg
– Head with 3 pairs of dark frontal setae; mouthparts capitate; wing pattern variable 177
177. Scutellum with apical marginal setae at least $^4/_5$ length of basal setae 178
– Scutellum with apical marginal setae at most $^1/_2$ length of basal setae 179
178. Wing pattern faintly reticulate (Fig. 174); head with frons setulose; ocellar triangle invariably bare; female postabdomen with oviscape black . . . . . *Tephritomyia* Hendel
– Wing pattern elongate/stellate (Fig. 176); head with frons bare; ocellar triangle with a few short basal setulae or bare; female postabdomen with oviscape reddish at base . . . . . *Trupanodesis* Merz
179. Head with frons and ocellar triangle strongly setulose; female postabdomen with oviscape reddish at base . . . . . *Pherothrinax* Munro
– Head with frons and ocellar triangle bare, or with a few short setulae above lunule; female postabdomen with oviscape black 180
180. Lower calypter much larger than upper calypter, convex on outer side . . . . . *Acanthiophilus* Becker
– Lower calypter very narrow, strap-like . . . . . *Tephrodesis* Merz [in part]
181. Wing very broad, strongly reticulate (Fig. 169); abdomen with paired maculae on tergites 3–5 . . . . . *Multireticula* Merz
– Wing narrow, not strongly reticulate (e.g., Figs 163, 164); abdomen non-maculate 182
182. Head without distinct facial carina, face flat to smoothly concave; scutellum with apical marginal setae short or absent; female postabdomen with oviscape uniformly dark . . . . . *Dectodesis* Munro
– Head with distinct facial carina; scutellum with apical marginal setae short; female postabdomen with oviscape reddish . . . . . *Freidbergia* Merz

Synopsis of the fauna

About 480 genera of Tephritidae are currently recognised globally, of which 160 occur in the Afrotropical Region. More than 4,930 valid species have been described from all zoogeographical regions except Antarctica, with *ca* 1,070 of these known from the Afrotropics. Several undescribed genera and numerous undescribed species are also known from the Afrotropical Region; some are noted in the above identification key and others in the text below and three are illustrated (Figs 129, 130, 144). No undescribed genera contain described species. Apart from some economically important species, few Afrotropical Tephritidae have had their immature stages described. Faunal checklists are available for Namibia (Hancock *et al*. 2001, 2003), United Arab Emirates (Merz 2008), Yemen (Merz *et al*. 2006), Zimbabwe (Hancock 2003*b*) and the Kakamega Region of western Kenya (Copeland *et al*. 2005). Merz & Dawah (2005) provided a checklist for neighbouring Palaearctic Saudi Arabia. Many genera, especially in the subfamily Tephritinae, lack modern identification keys to species and identification usually requires comparison with illustrated or determined taxa. Papers by Bezzi (1924*a*, *b*) and Munro (listed below) are useful starting points.

Acanthiophilus Becker (Tephritinae: Tephritini)**.** A genus of eight described species occurring in the Afrotropical, Oriental and Palaearctic Regions. Six species occur in the continental Afrotropics, including the widespread *A. helianthi*, also recorded from the Oriental and Palaearctic Regions. Larvae develop in flower heads of Asteraceae: Cardueae. Morgulis *et al*. (2015) provided descriptions of the larva and puparium of *A. brunneus* Munro, 1934 and an identification key to species.

Acidoxantha Hendel (Trypetinae: Acidoxanthini)**.** A genus of nine described species occurring in the Afrotropical, Australasian and Oriental Regions. One species occurs in the Afrotropics, *A. bisinuata* Hancock, 1985, described from Madagascar. Larvae of some Oriental species develop in the buds of large flowers, such as *Bauhinia* (Leguminosae), *Bombax* (Bombacaceae) and *Hibiscus* (Malvaceae). Biology and immature stages otherwise remain unknown. The Afrotropical species can be identified by reference to Hancock (1985*a*).

Acidoxanthopsis Hering (Trypetinae: Acidoxanthini)**.** An endemic genus of one described species, *A. advena* Hering, 1941 (Fig. 33), from Tanzania and two undescribed species from Cameroon and Kenya, respectively. Biology and immature stages remain unknown. The genus is in need of revision and no identification key to species is currently available.

Aciura Robineau-Desvoidy (Tephritinae: Tephrellini)**.** A genus of two described species occurring in the Afrotropical and Palaearctic Regions. One Palaearctic species, *A. afghana*

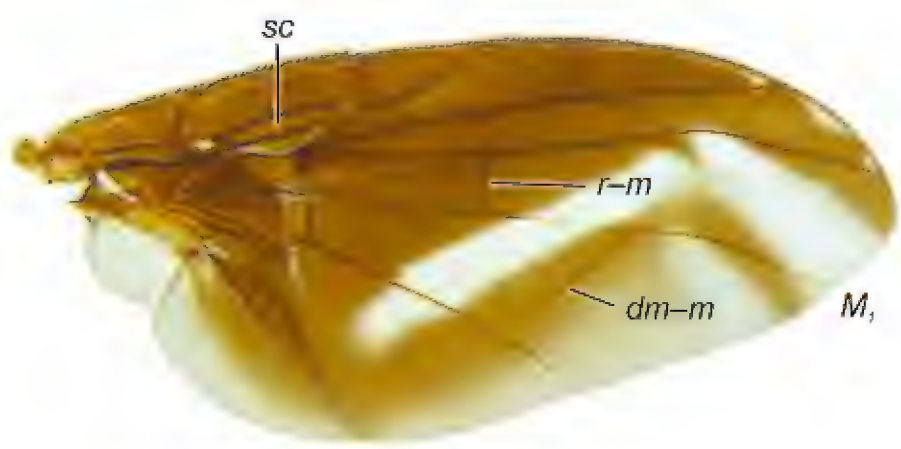
(Hering, 1961), extends into United Arab Emirates in the Afrotropical part of the Arabian Peninsula. Larvae develop in flower heads of *Ballota* and *Phlomis* (Lamiaceae). Biology and immature stages otherwise remain unknown. The Afrotropical species can be identified by reference to Merz (2008).

Acronneus Munro (Tephritinae: Tephritini)**.** An endemic monotypic genus, with the single described species, *A. bryanti* (Munro, 1929) (Fig. 153), recorded from Kenya and South Africa. The genus belongs in the *Sphenella*-group. Biology and immature stages remain unknown.

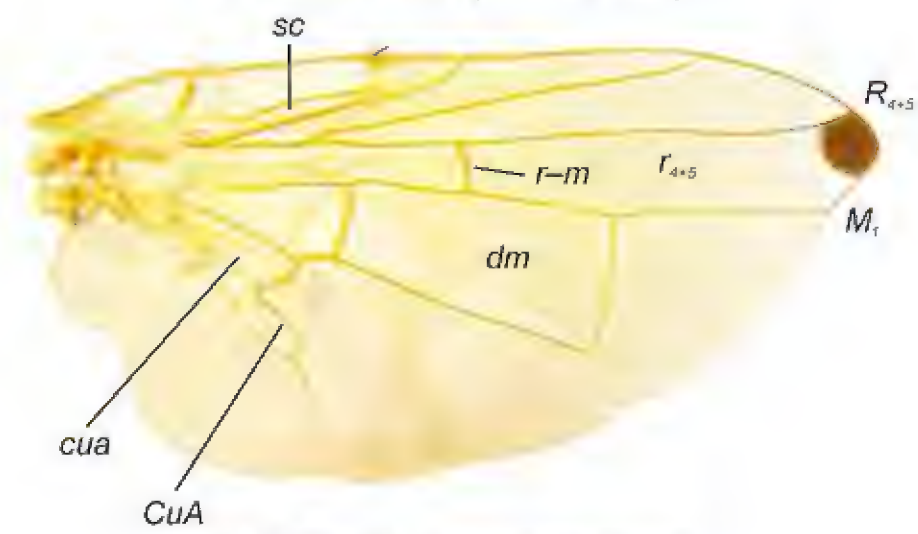
Actinoptera **Rondani** (Tephritinae: Tephritini)**.** A genus of 29 described and two undescribed species (Fig. 161) occurring in the Afrotropical, Oriental and Palaearctic Regions. Fourteen species occur in the Afrotropics, of which four are known from the Indian Ocean islands: *A. tuckeri* (Bezzi, 1924) (Fig. 162) from Madagascar and South Africa; two undescribed species from Madagascar; and *A. vinsoni* from Mauritius, although the last named species has a longer pterostigma, more posteriorly placed dorsocentral setae and three pairs of frontal setae and appears to be better placed in *Euarestella*. Larvae develop in flower heads or stems of *Helichrysum*, *Filago* and *Gnaphalium*

46 *Bactrocera* (*Bactrocera*)

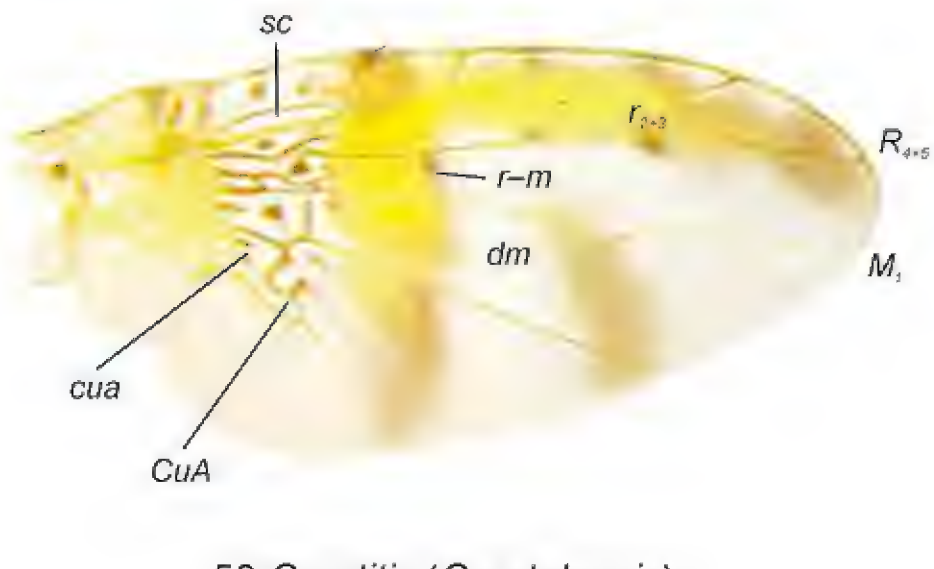
47 *Bactrocera* (*Javadacus*)



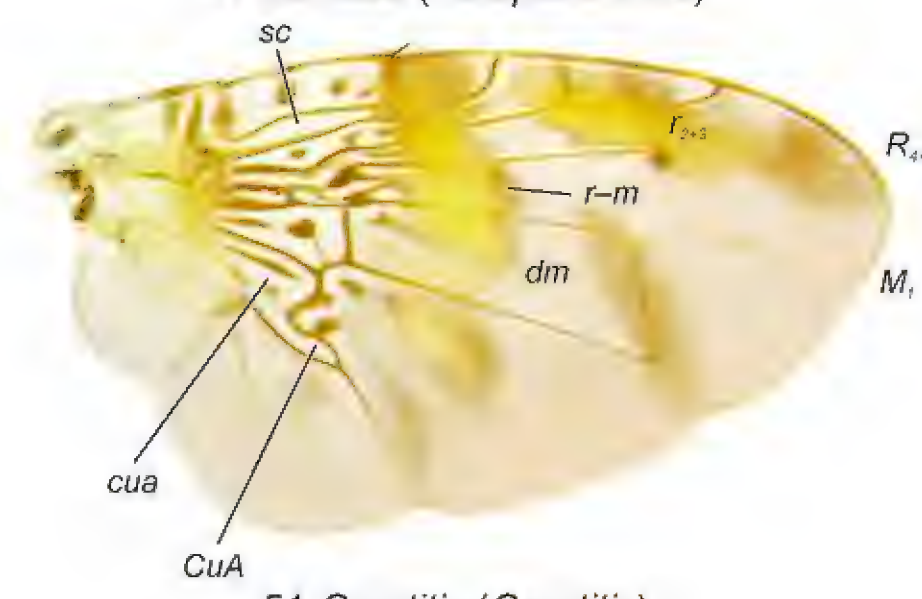
48 *Carpophthoromyia*



49 *Ceratitis* (*Acropteromma*)



50 *Ceratitis* (*Ceratalaspis*)



51 *Ceratitis* (*Ceratitis*)

Figs 71.46–51. Wings of Tephritidae (dorsal views): (46) *Bactrocera* (*Bactrocera*) *invadens* Drew, Tsuruta & White; (47) *B.* (*Javadacus*) *cucurbitae* (Coquillett); (48) *Carpophthoromyia vittata* (F.); (49) *Ceratitis* (*Acropteromma*) *munroanum* (Bezzi); (50) *C.* (*Ceratalaspis*) *cosyra* (Walker); (51) *C.* (*Ceratitis*) *capitata* (Wiedemann). Figs 46, 47 (photographs © K.J. David).

Abbreviations: *bm* – basal medial cell; *CuA* – anterior branch of cubital vein; *cua* – anterior cubital cell; *dm* – discal medial cell; *dm–m* – discal medial crossvein; M_1 – first branch of media; r_{2+3} – second + third radial cell; r_{4+5} – fourth + fifth radial cells; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *sc* – subcostal cell.

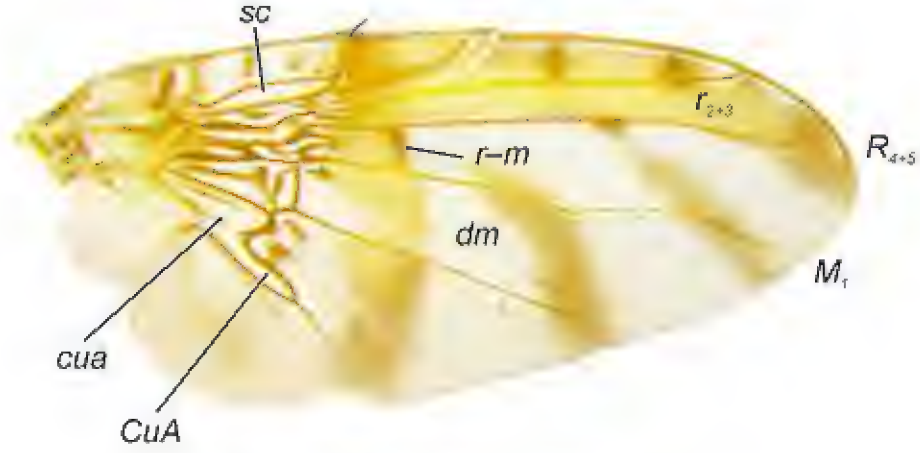
(Asteraceae: Inuleae). Biology and immature stages otherwise remain unknown. Munro (1957*a*) provided an identification key to species.

***Aethiothemara* Hendel** (Phytalmiinae: Acanthonevrini)**.** An endemic genus of six species (Fig. 19) recorded from Cameroon to Kenya and Tanzania. Biology and immature stages remain unknown. Hancock (2015) provided an identification key to species.

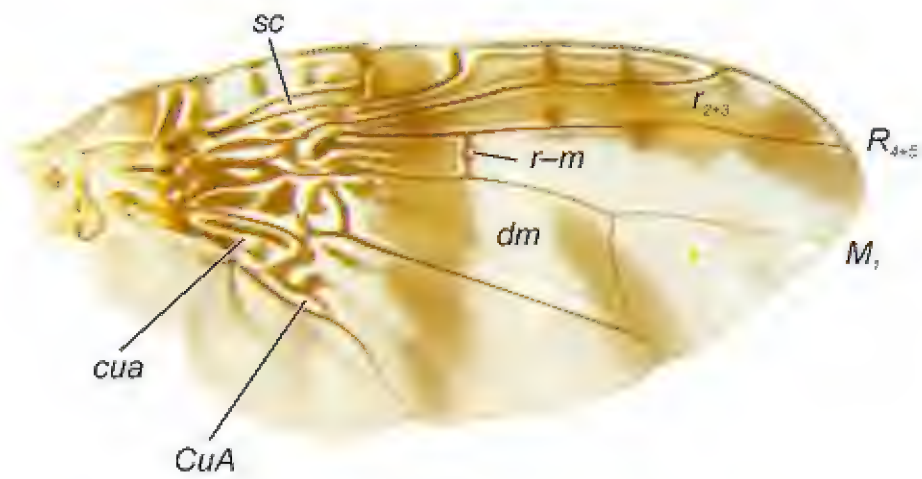
***Afraciura* Hering** (Tephritinae: Tephrellini)**.** An endemic genus of four described species (Fig. 94) from East and Southern Africa. Larvae develop in the flower heads of *Lantana* and *Lippia* (Verbenaceae). Biology and immature stages otherwise remain unknown. Munro (1947) provided an identification key to species (as *Conionota*).

***Afrocneros* Bezzi** (Phytalmiinae: Acanthonevrini)**.** An endemic Southern African genus of three described species: *A. excellens* (Loew, 1860) (Fig. 20), recorded from South Africa and Zimbabwe; *A. mundissimus* Bezzi, 1924, from South Africa; and *A. mundus* (Loew, 1863), from Lesotho and South Africa. Larvae develop beneath the bark of *Cussonia* (Araliaceae) trees. Biology and immature stages otherwise remain unknown. Munro (1967) provided an identification key to species.

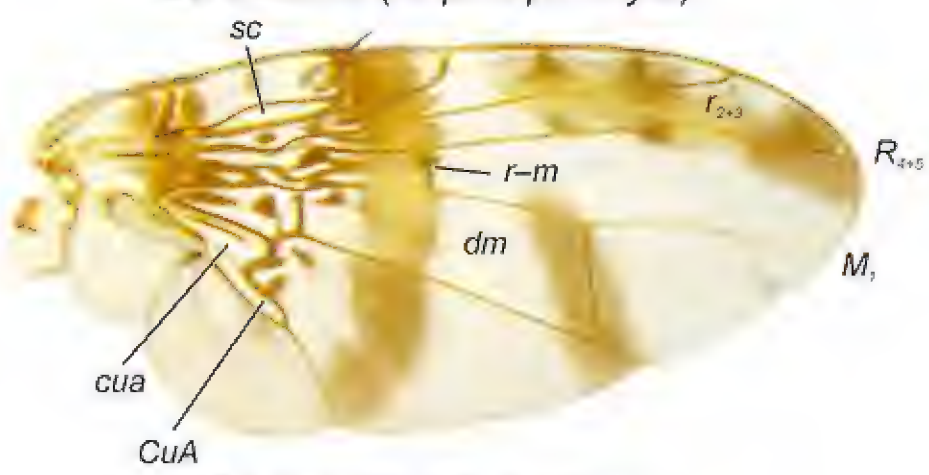
***Afreutreta* Bezzi** (Tephritinae: Eutretini)**.** A genus of one Oriental and three described Afrotropical species: *A. bipunctata*



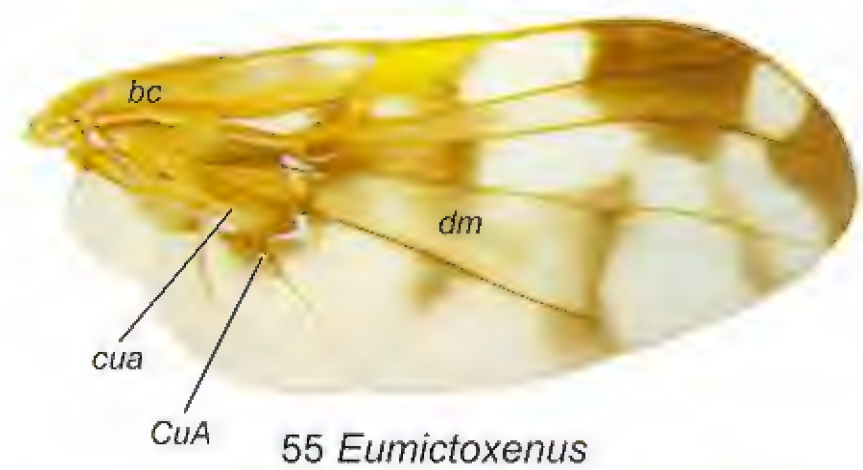
52 *Ceratitis* (*Hoplolophomyia*)



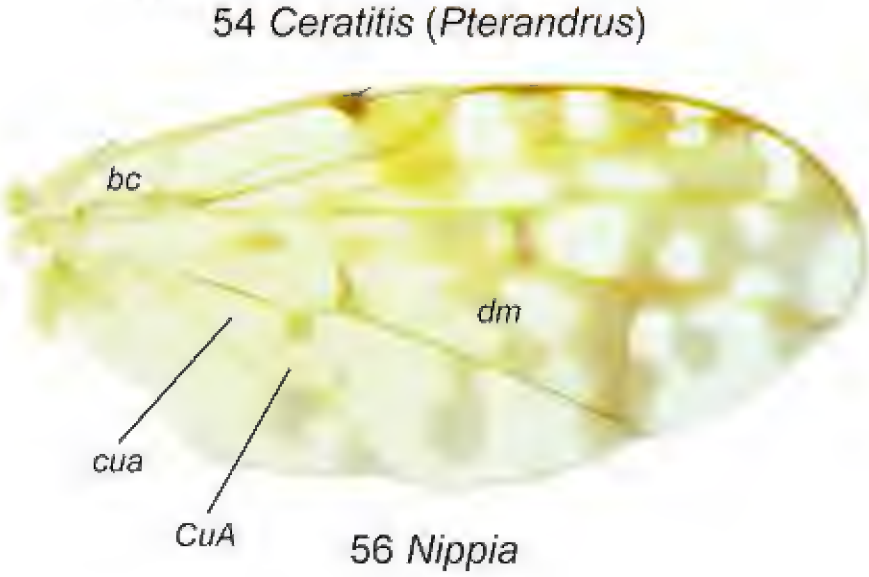
53 *Ceratitis* (*Pardalaspis*)



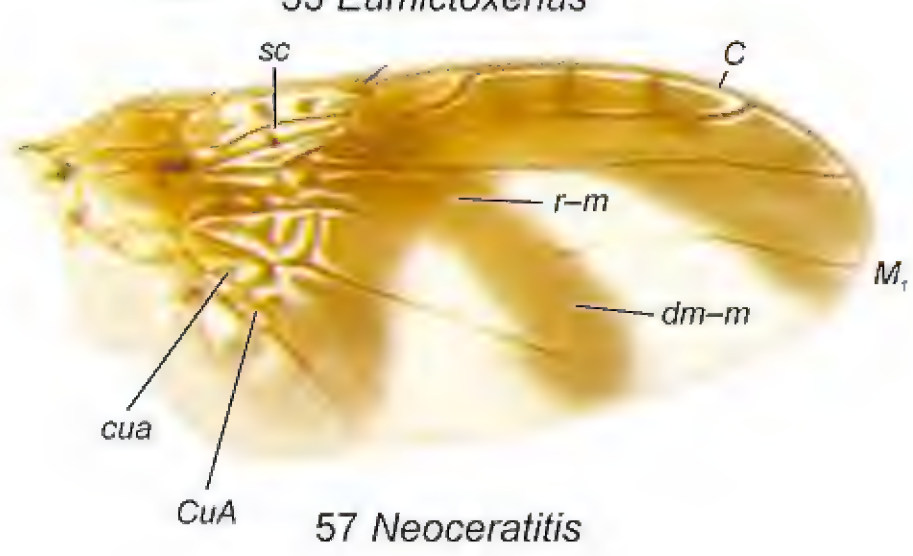
54 *Ceratitis* (*Pterandrus*)



55 *Eumictoxenus*



56 *Nippia*



57 *Neoceratitis*

Figs 71.52–57. Wings of Tephritidae (dorsal views): (52) *Ceratitis* (*Hoplolophomyia*) *cristata* (Bezzi); (53) *C.* (*Pardalaspis*) *punctata* (Wiedemann); (54) *C.* (*Pterandrus*) *rosa* Karsch; (55) *Eumictoxenus leleupi* Munro; (56) *Nippia* sp.; (57) *Neoceratitis efflatouni* (Hendel).

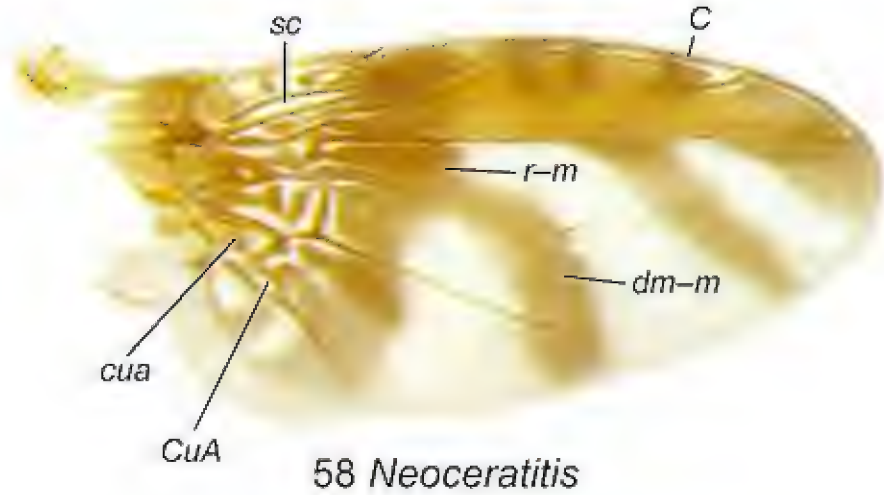
Abbreviations: *bc* – basal costal cell; *C* – costal vein; *CuA* – anterior branch of cubital vein; *cua* – anterior cubital cell; *dm* – discal medial cell; *dm–m* – discal medial crossvein; M_1 – first branch of media; r_{2+3} – second + third radial cell; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *sc* – subcostal cell.

(Loew, 1861) (Fig. 13) and *A. hemimelas* (Bezzi, 1926) from South Africa; and *A. muiri* (Bezzi, 1924), from Mozambique and South Africa. The Oriental species, *A. magna* (Hardy, 1988) from Java, Indonesia, was included by Hancock (2007*b*). The eutretine genera *Afreutreta*, *Cosmetothrix* and *Tarchonanthea* all appear to be related to the Nearctic/Neotropical genus *Eutreta* Loew. Larvae of Afrotropical species develop in twig galls on *Brachylaena* (Asteraceae). Biology and immature stages otherwise remain unknown. Freidberg & Kaplan (1993) provided an identification key to species.

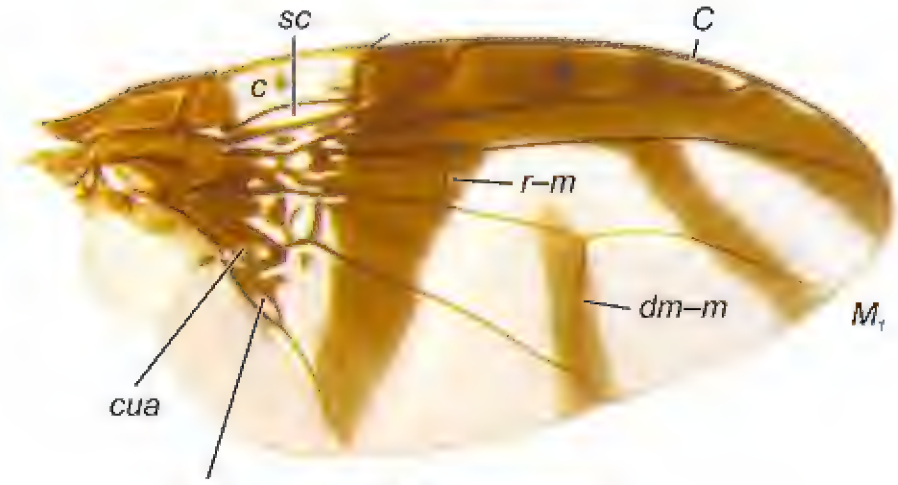
***Antoxya* Munro** (Tephritinae: Tephritini)**.** An endemic monotypic genus, with the only described species, *A. oxynoides* (Bezzi, 1924) (Fig. 131), recorded from Ethiopia, Kenya, Tanzania and Uganda. Biology and immature stages remain unknown.

***Arabodesis* Merz & Dawah** (Tephritinae: Tephritini)**.** An endemic genus, with the single described species, *A. reductiseta* Merz & Dawah, 2005, from Saudi Arabia and Yemen in the Arabian Peninsula and an additional undescribed species from Yemen (Merz *et al*. 2006). Biology and immature stages remain unknown.

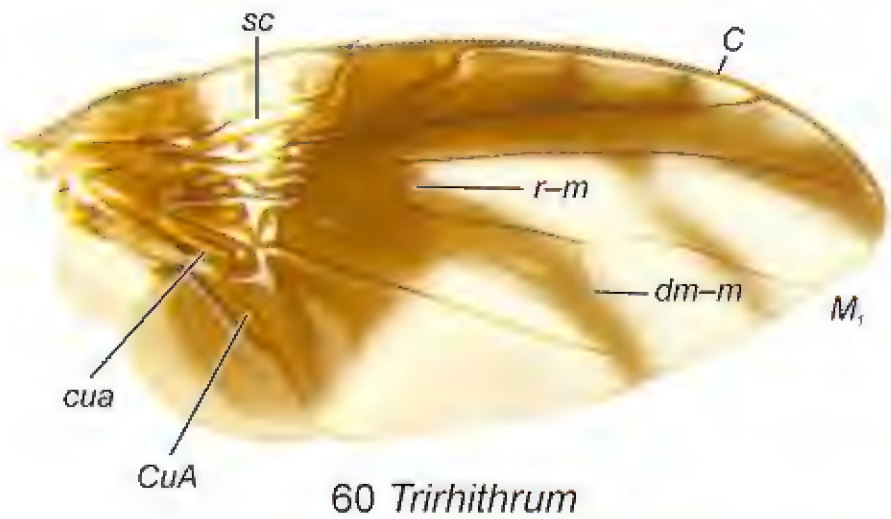
***Asimoneura* Czerny** (Tephritinae: Myopitini)**.** A genus of 4 described and at least 25 undescribed species, restricted to the



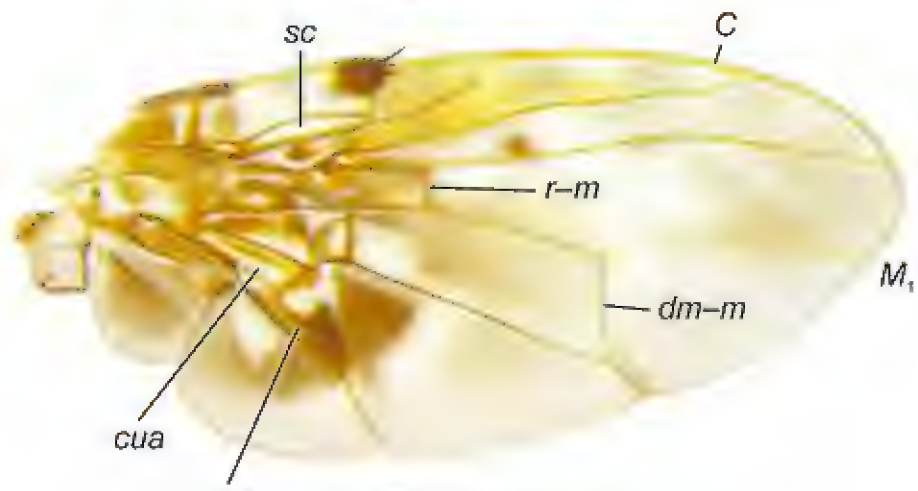
58 *Neoceratitis*



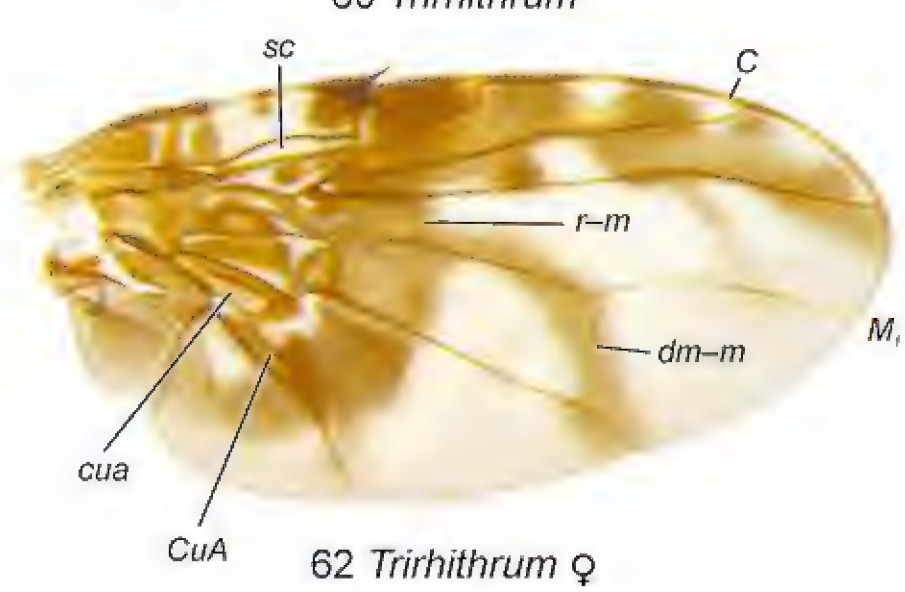
59 *Perilampsis*



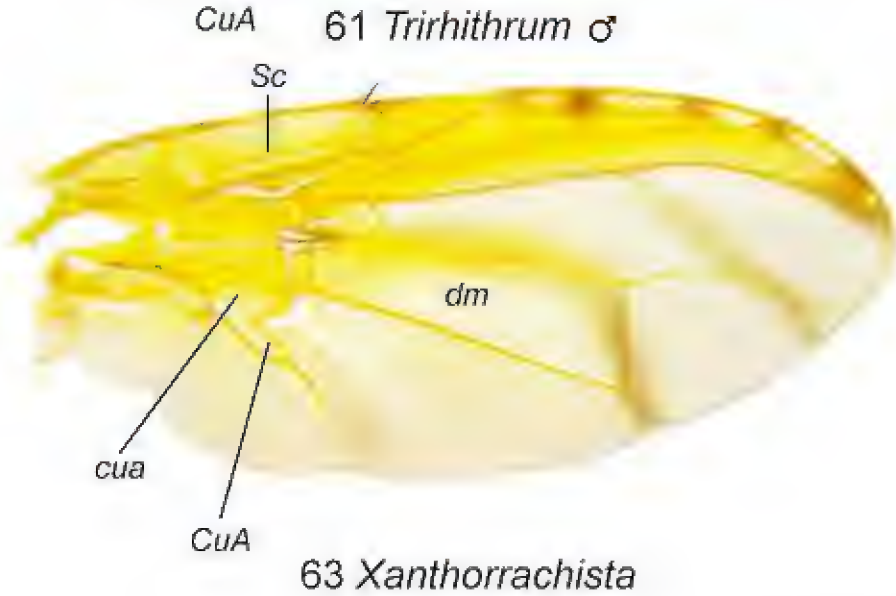
60 *Trirhithrum*



61 *Trirhithrum* ♂



62 *Trirhithrum* ♀



63 *Xanthorrachista*

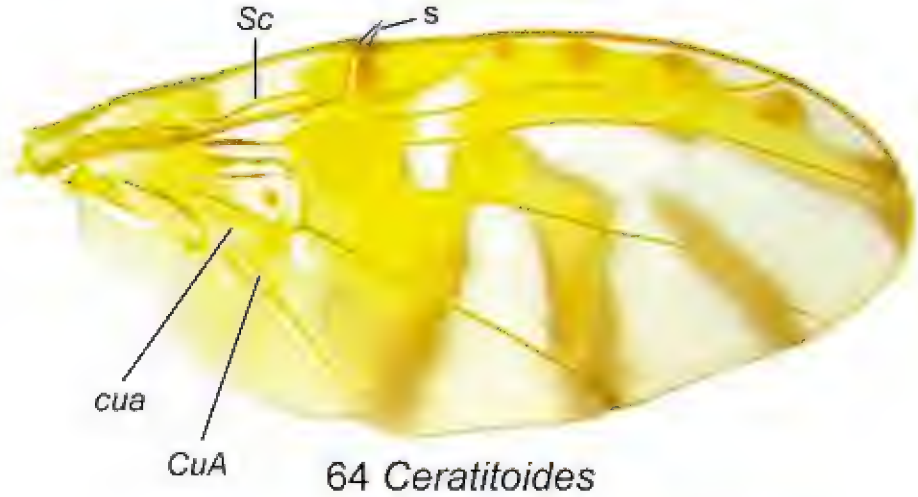
Figs 71.58–63. Wings of Tephritidae (dorsal views): (58) *Neoceratitis lycii* (Coquillett); (59) *Perilampsis pulchella* (Austen); (60) *Trirhithrum stecki* White; (61) *T. coffeae* Bezzi ♂; (62) same, ♀; (63) *Xanthorrachista alata* (Becker).

Abbreviations: *c* – costal cell; *C* – costal vein; *CuA* – anterior branch of cubital vein; *cua* – anterior cubital cell; *dm* – discal medial cell; *dm–m* – discal medial crossvein; M_1 – first branch of media; *r–m* – radial–medial crossvein; *sc* – subcostal cell; *Sc* – subcostal vein.

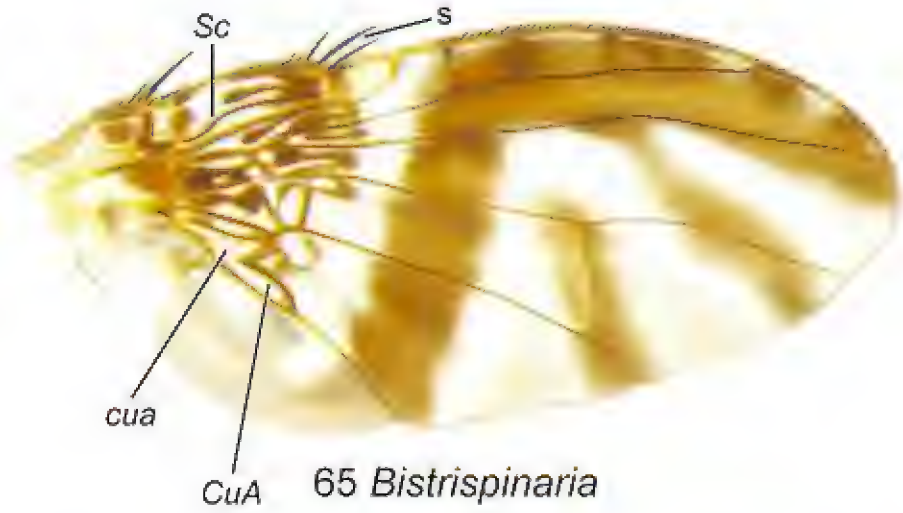
Afrotropical and Palaearctic Regions. An Oriental species, "*A.*" *shirakii* (Munro, 1935) belongs elsewhere (V.A. Korneyev, pers. comm. 2020). The three described Afrotropical species are: *A. indecora* (Loew, 1861), from South Africa and Zimbabwe; *A. pantomelas* (Bezzi, 1926) (Fig. 70), from South Africa, Tanzania and Zimbabwe; and *A. petiolata* (Munro, 1931), from South Africa. The 25 undescribed species are known from East and Southern Africa, although species with wing veins R_{4+5} and M_1 convergent and an apical macula possibly belong in an additional, undescribed genus. Larvae develop in flower heads of *Helichrysum* and *Pentzia* (Asteraceae). Biology and immature stages otherwise remain unknown. Freidberg & Norrbom (1999: 601) reviewed the genus, but no identification key to species was provided.

***Axiothauma* Munro** (Tephritinae: Axiothaumini)**.** An endemic genus of three described species: *A. albinodosum* Munro, 1946, *A. edwardsi* Munro, 1946 and *A. nigritens* Munro, 1946, all from higher elevations (3,000–4,300 m) in Kenya. Larvae develop in galls on *Senecio* (Asteraceae). Biology and immature stages otherwise remain unknown. Munro (1946) provided an identification key to species.

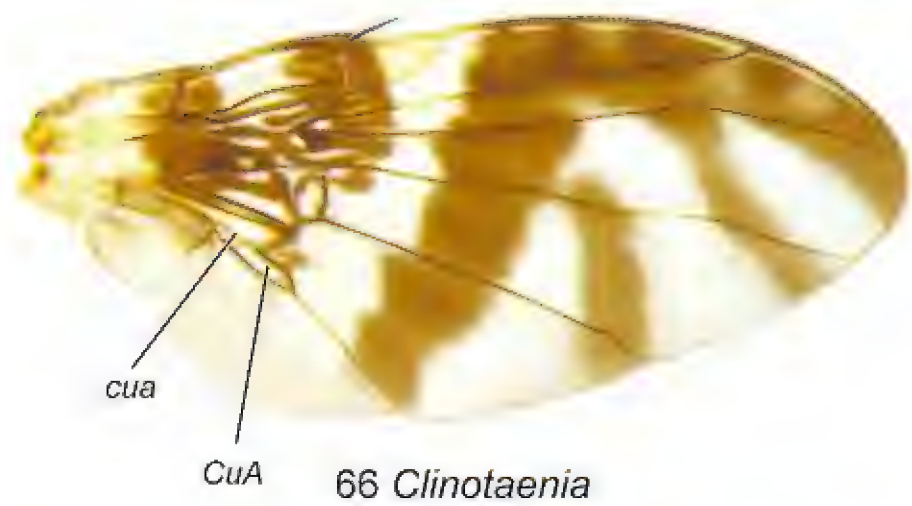
***Bactrocera* Macquart** (Dacinae: Dacini)**.** A largely Oriental and Australasian genus of *ca* 660 described species, plus numerous undescribed species. Some 15 species occur in the Afrotropics, 11 endemic (with one, *B.* (*Daculus*) *oleae* (Rossi, 1790), adventive in the Nearctic, western Oriental and Palaearctic Regions) and four adventives of Oriental (Indian)



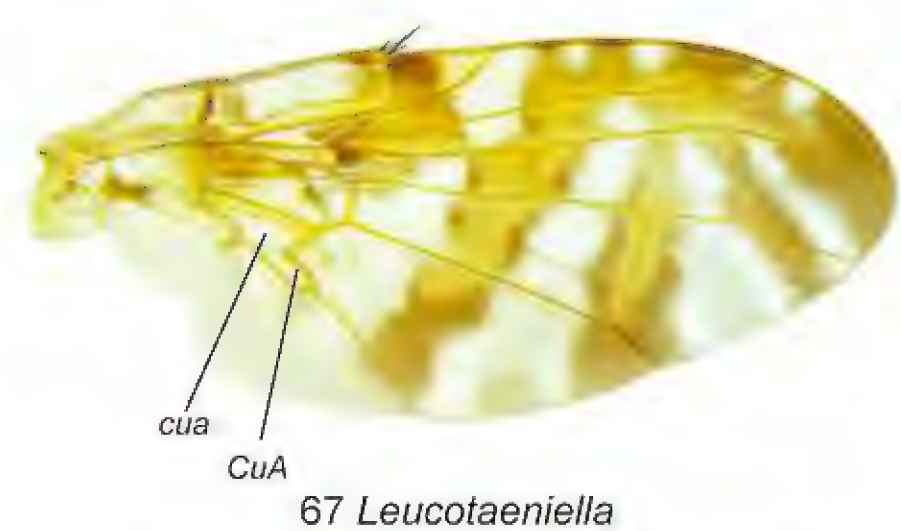
64 *Ceratitoides*



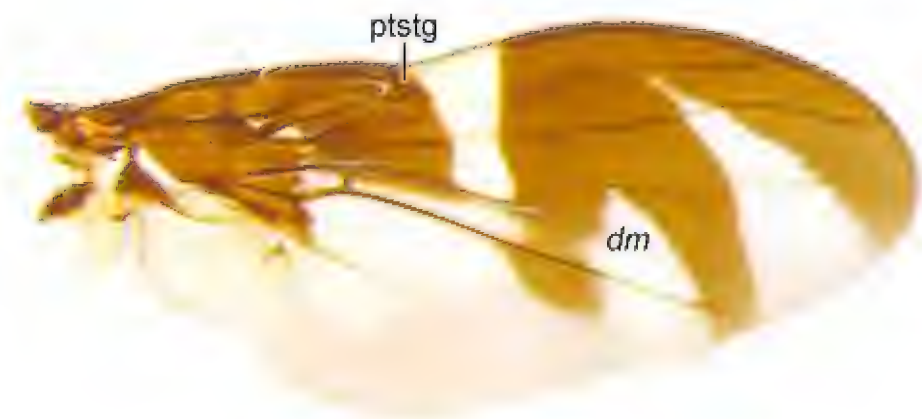
65 *Bistrispinaria*



66 *Clinotaenia*



67 *Leucotaeniella*



68 *Zacerata*

69 *Craspedoxantha*

Figs 71.64–69. Wings of Tephritidae (dorsal views): (64) *Ceratitoides nigromaculatus* Hendel; (65) *Bistrispinaria fortis* (Speiser); (66) *Clinotaenia camerunica* Hancock; (67) *Leucotaeniella trispila* Bezzi; (68) *Zacerata asparagi* Coquillett; (69) *Craspedoxantha* sp.

Abbreviations: *CuA* – anterior branch of cubital vein; *cua* – anterior cubital cell; *dm* – discal medial cell; ptstg – pterostigma; s – setae; *Sc* – subcostal vein.

origin. The endemic species were assigned to two subgenera, *B.* (*Daculus* Speiser) (= *Afrodacus* Bezzi) and *B.* (*Gymnodacus* Munro), by White (2006) and three by Hancock & Drew (2015), who placed *B. nesiotes* Munro, 1984 in the monotypic Madagascan subgenus *B.* (*Aglaodacus* Munro); the well-developed supernumerary lobe on the male wing is typical of the *Zeugodacus* group of subgenera and unlike the condition expressed in the *Melanodacus* group of subgenera, to which *B.* (*Daculus*) and *B.* (*Gymnodacus*) belong; it also lacks the dark anatergite expressed in all *B.* (*Daculus*) and *B.* (*Gymnodacus*) species. The adventive species belong in the subgenera *Bactrocera sensu stricto* and *B.* (*Javadacus* Hardy), the latter also belonging in the *Zeugodacus* group of subgenera. *Zeugodacus* Hendel is regarded as a separate genus by some authors, based solely on molecular evidence that is not supported by morphology, biology or molecular clock dating (see discussion in Hancock & Drew 2018*a*, *b*). The adventive species are *B.* (*B.*) *invadens* (Fig. 46), a now widespread species first recorded from Mauritius in 1996 and Kenya in 2003 and often regarded as a synonym of the Oriental *B.* (*B.*) *dorsalis* (Hendel, 1912), but with narrower postsutural lateral yellow vittae and a very different pattern of scutal variation (Drew & Romig 2016: 3) (there are also differences in phallus structure and aculeus length), *B.* (*B.*) *latifrons* (Hendel, 1915), first recorded in Tanzania in 2006 and *B.* (*B.*) *zonata* (Saunders, 1842), present in Mauritius since at least 1942, Réunion Is. since at least 2001 and on the Arabian Peninsula since at least the early 1980s, plus *B.* (*J.*) *cucurbitae* (Coquillett, 1899) (Fig. 47), present in East Africa since at least 1930 and now known from much of East and West Africa, Mauritius, Réunion Is. and Seychelles (White 2006; White & Goodger 2009). A record of *B.* (*B.*) *caryeae* (Kapoor, 1971) from Oman (Drew & Hancock 1994) is regarded as a quarantine interception; the record has not been repeated. Larvae of most species develop in fleshy fruits: *B.* (*B.*) *invadens* and *B.* (*B.*) *zonata* are highly polyphagous pest species; *B.* (*B.*) *latifrons* is a pest of Solanaceae, *B.* (*J.*) *cucurbitae* of Cucurbitaceae and *B.* (*D.*) *oleae* of olives (Oleaceae). Males of the endemic species show no response to male attractants, whereas most of the adventive species respond strongly to either methyl eugenol (*B.* (*B.*) *invadens* and *B.* (*B.*) *zonata*) or cue-lure (*B.* (*J.*) *cucurbitae*). Descriptions of third-instar larvae (except *B. invadens*) were provided by White & Elson-Harris (1992: 210, 240, 242, 269) and White (2006) provided an identification key to most Afrotropical species. Oriental species, including the adventives, were keyed by Drew & Romig (2016: 37).

***Bactropota* Bezzi** (Tephritinae: Schistopterini)**.** A small genus containing one described Afrotropical species, *B. woodi* Bezzi, 1924 (Fig. 82), occurring in much of the continental Afrotropics, plus one undescribed species from Saudi Arabia in the Palaearctic (Merz & Dawah 2005) and one from Madagascar. Larvae of *B. woodi* develop in flower heads of *Pluchea dioscoridis* (L.) DC (Asteraceae: Inuleae). Biology and immature stages otherwise remain unknown. The genus is in need of revision and no identification ley to species is currently available.

***Baryglossa* Bezzi** (Blepharoneurinae)**.** An endemic genus of seven described species (Figs 17, 18), distributed from Togo and Cameroon to Eritrea and Kenya. *Baryglossa tersa* Munro, 1939 has been reared from flowers of a cucurbit (Cucurbitaceae) and adults of other species have been collected on flowering cucurbits. Biology and immature stages otherwise remain unknown. Munro (1957*a*) provided an identification key to species.

***Bezzina* Munro** (Tephritinae: Pliomelaenini)**.** An endemic monotypic genus, with the single described species, *B. margaretifera* (Bezzi, 1908) (Fig. 132), recorded from East, north-east and Southern Africa and Madagascar. Larvae develop on an unidentified species of Acanthaceae. Biology and immature stages otherwise remain unknown. Of previously uncertain placement, the genus is here provisionally referred to the Pliomelaenini, based on its acanthaceous host-plant.

***Bibundia* Bischof** (Tachiniscinae: Tachiniscini)**.** An endemic genus of two described species, *B. fenestrata* (Grünberg, 1906) (Fig. 16), from Sierra Leone and Togo and *B. hermanni* Bischof, 1903, from Cameroon and Democratic Republic of Congo. An unidentified species has been reared from saturniid moth caterpillars in Nigeria (Roberts 1969). Biology and immature stages otherwise remain unknown. Korneyev & Norrbom (2006) provided detailed re-descriptions and an identification key to species.

***Bistrispinaria* Speiser** (Dacinae: Gastrozonini)**.** An endemic genus of four described species (Fig. 65) known from East, West and Southern Africa. Larvae develop in the shoots of panicoid grasses (Poaceae) (Copeland 2007; Hancock 1999). Biology and immature stages otherwise remain unknown. Hancock (1999) provided an identification key to species.

***Brachiopterna* Bezzi** (Tephritinae: Schistopterini)**.** An endemic genus containing two described species, *B. katonae* Bezzi, 1924 (Fig. 83) from Kenya and Tanzania and *B. ornithomorpha* from Niger and Ethiopia to South Africa, plus an undescribed species from Tanzania. Larvae of the three known species develop in flower heads of *Sphaeranthus bullatus* Mattf., *S. suaveolens* (Forssk.) DC. and *S. cyathuloides* O.Hoffm. (Asteraceae: Plucheae), respectively. Biology and immature stages otherwise remain unknown. No identification key to species is currently available.

***Brachyaciura* Bezzi** (Tephritinae: Tephrellini)**.** An endemic genus of three described species: *B. kovacsi* Bezzi, 1924 (Fig. 107), from Ethiopia and Kenya; *B. limbata* (Bezzi, 1924), from Uganda and possibly Kenya; and *B. rufiventris* (Bezzi, 1918) from Eritrea and Sudan, plus probably two undescribed species from Ethiopia. Larvae develop in seeds of *Acanthus* (Acanthaceae). Biology and immature stages otherwise remain unknown. Munro (1947) provided an identification key to described species.

***Brachydesis* Hancock** (Tephritinae: Tephritini)**.** An endemic monotypic genus, with the single described species, *B. rivularis* (Bezzi, 1924) (Fig. 160), from South Africa. This genus is closely related to *Actinoptera* and *Brachytrupanea*, all three having a very short pterostigma (Merz 1999: 640). Biology and immature stages remain unknown.

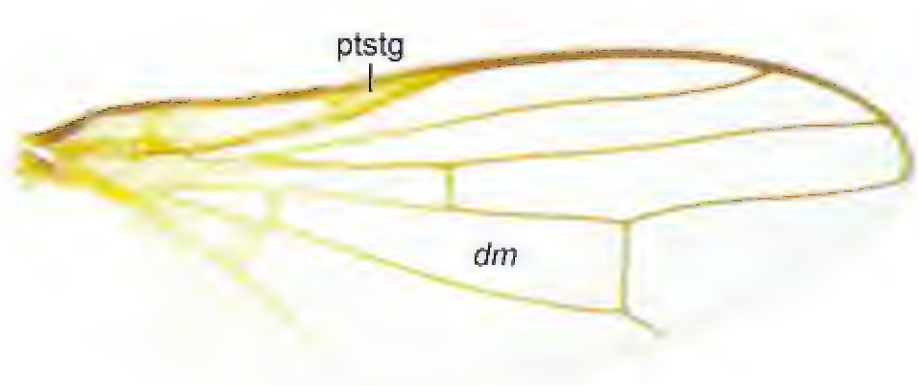
***Brachytrupanea* Hancock** (Tephritinae: Tephritini)**.** An endemic genus of two described species: *B. brachystigma* (Bezzi, 1924) from Malawi and South Africa; and *B. semiatrata* (Hering, 1942) from Tanzania. Biology and immature stages remain unknown. No identification key to species is currently available.

***Campiglossa* Rondani** (Tephritinae: Tephritini)**.** A virtually cosmopolitan genus of *ca* 178 described species occurring in

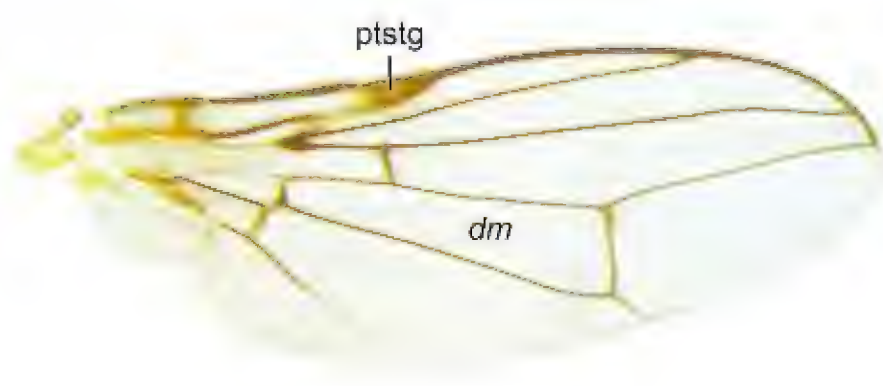
all zoogeographical regions except Antarctica. At least 28 species occur in the continental Afrotropics, with one, *C. ignobilis* (Loew, 1861) (Fig. 135), also recorded from Yemen and Palaearctic Saudi Arabia in the Arabian Peninsula. An additional undescribed species is known from Madagascar. Larvae develop in flower heads of Asteraceae. Biology and immature stages of Afrotropical species otherwise remain unknown. Munro (1957a) provided an identification key to 26 species (as *Paroxyna*), to which should be added *C. suboculata* (Séguy, 1939) and *C. zavattarii* (Séguy, 1939) from Ethiopia (Séguy 1939). The genus is in need of revision with relation to other *Campiglossa* group genera, some of which (e.g., *Dioxyna*: see below) were recently synonymised (Han & Ro 2019).

***Capitites* Foote & Freidberg** (Tephritinae: Tephritini)**.** A genus of three described species occurring in the Afrotropical and Palaearctic Regions. Three species are Afrotropical: *C. albicans* (Munro, 1935) from South Africa; *C. dentiens* (Bezzi, 1924), recorded from South Africa and Zimbabwe; and *C. augur* (Frauenfeld, 1857), known from the southern Palaearctic to Sudan. Larvae develop in flower heads of *Phagnalon* and *Pulicaria* (Asteraceae: Inuleae). Biology and immature stages otherwise remain unknown. No identification key to species is currently available.

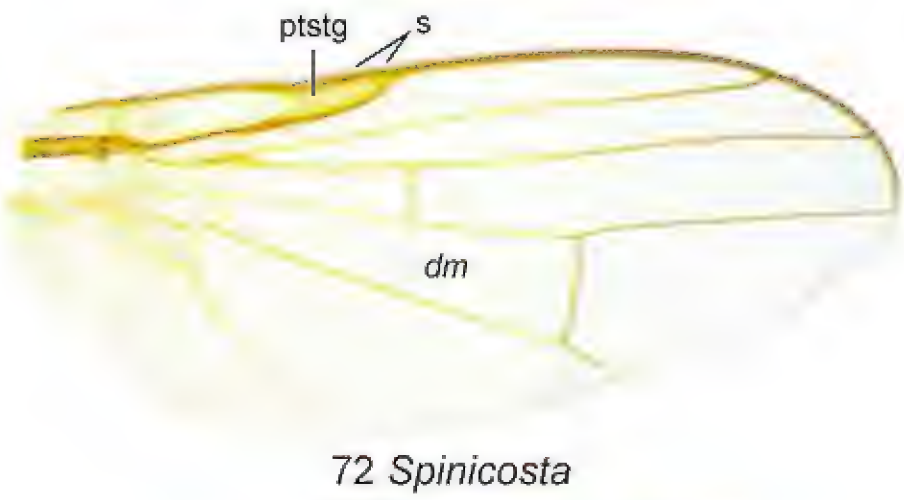
***Capparimyia* Bezzi** (Dacinae: Ceratitidini)**.** A predominantly Afrotropical genus of eight described species occurring in the Afrotropical, Oriental (Pakistan) and Palaearctic Regions. The widespread species *C. aenigma* De Meyer & Freidberg, 2005, is recorded from Kenya, Namibia, Tanzania and tentatively Saudi Arabia, while the Mediterranean species *C. savastani* (Martelli, 1910) occurs in Oman and Yemen in the Afrotropics. The remaining six species all occur in the continental Afrotropics. Larval hosts are the buds and fruit of Capparaceae. Biology



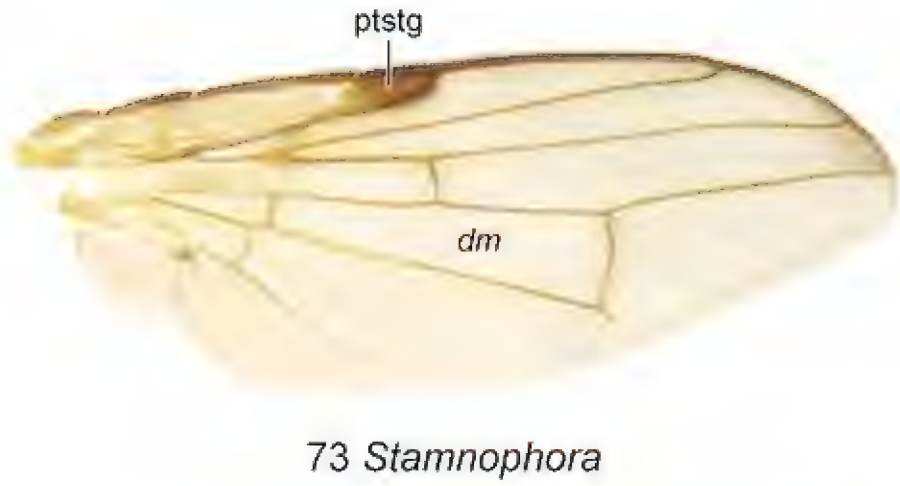
70 *Asimoneura*



71 *Myopites*

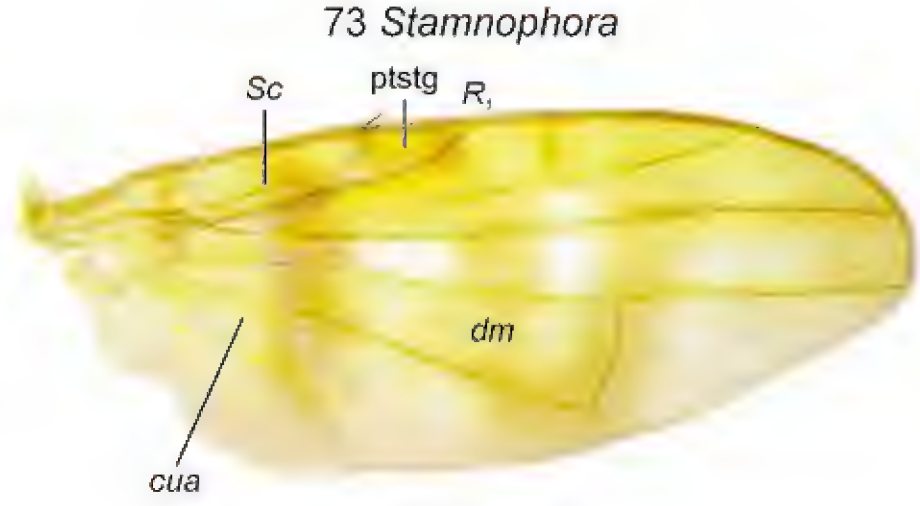


72 *Spinicosta*



73 *Stamnophora*

74 *Urophora*



75 *Cryptophorellia*

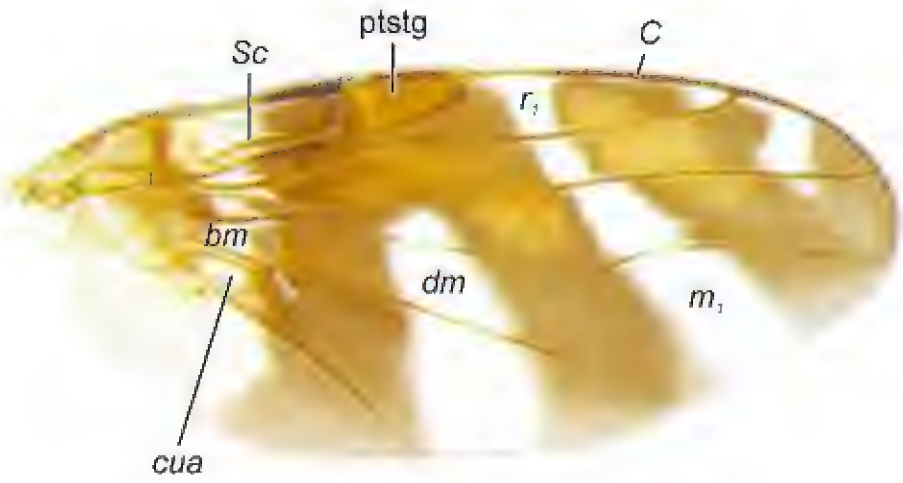
Figs 71.70–75. Wings of Tephritidae (dorsal views): (70) *Asimoneura pantomelas* (Bezzi); (71) *Myopites delottoi* Munro; (72) *Spinicosta cilipennis* (Bezzi); (73) *Stamnophora vernoniicola* (Bezzi); (74) *Urophora* sp.; (75) *Cryptophorellia longicauda* Freidberg & Hancock.

Abbreviations: *cua* – anterior cubital cell; *dm* – discal medial cell; ptstg – pterostigma; R_1 – anterior branch of radius; s – setae; *Sc* – subcostal vein.

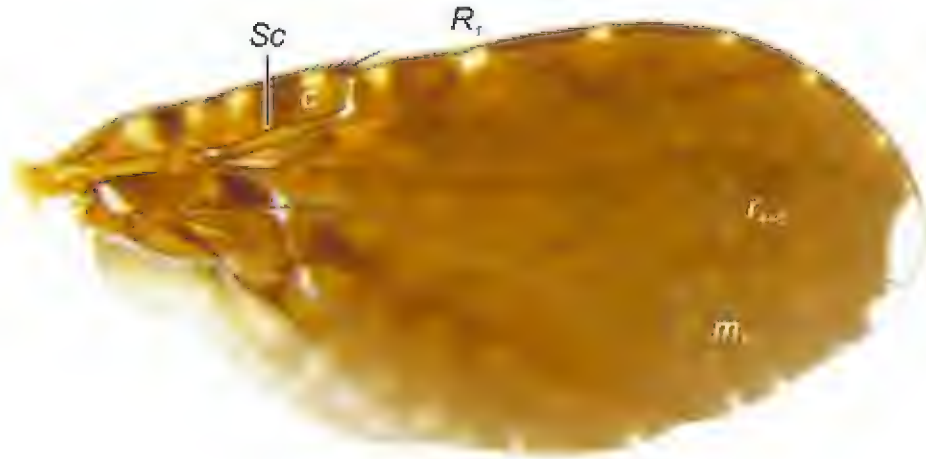
and immature stages otherwise remain unknown. De Meyer & Freidberg (2005) provided an identification key to species.

***Carpomya* Costa** (Trypetinae: Carpomyini)**.** A genus of three described species occurring in the Afrotropical, Oriental and Palaearctic Regions. *Myiopardalis* is considered a subgenus or synonym by some authors. *Carpomya incompleta* (Becker, 1903) extends into the Afrotropics as far south as Ethiopia and United Arab Emirates and *C. vesuviana* Costa, 1854 is also recorded from United Arab Emirates. Larvae develop in the fruit of *Rosa* (Rosaceae) or *Zizyphus* (Rhamnaceae). For partial descriptions of the third-instar larvae and an identification key to species see Kandybina (1977) and White & Elson-Harris (1992: 92).

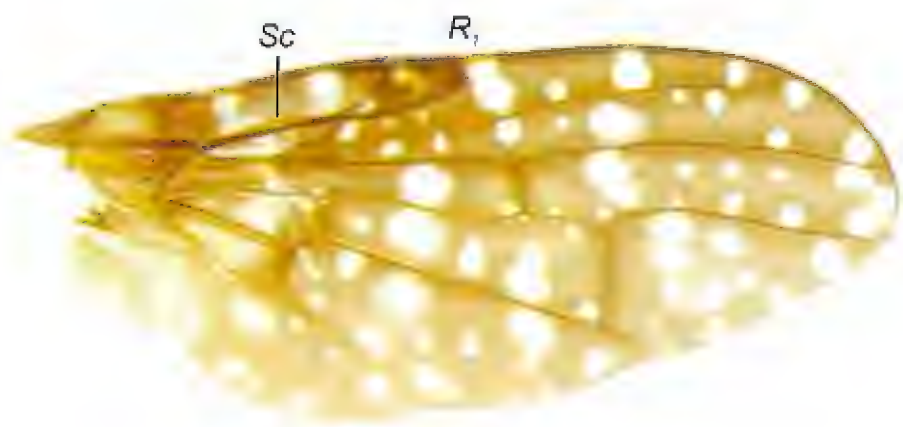
***Carpophthoromyia* Austen** (Dacinae: Ceratitidini)**.** An endemic genus of 17 described species (Fig. 48), with 16 species recorded from East, Southern and West Africa and one, *C. speciosa* Hancock, 1984, from Madagascar. Larvae develop primarily in the fruit of *Drypetes* (Euphorbiaceae); other records are unconfirmed. Biology and immature stages otherwise remain



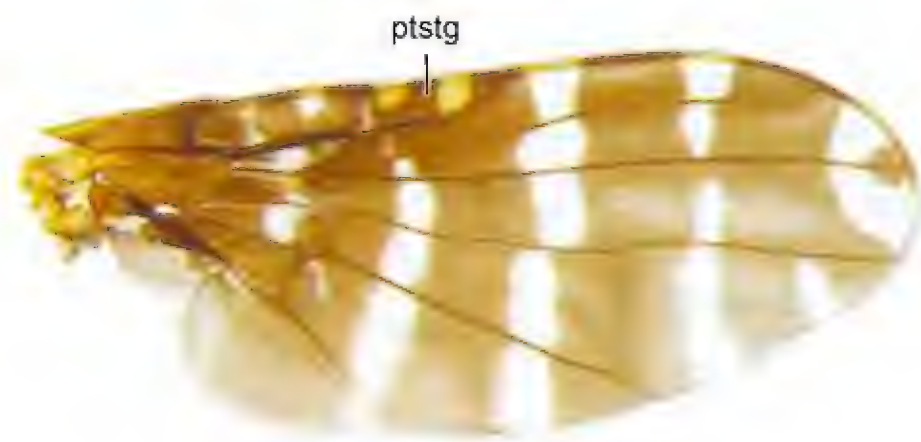
76 *Procecidochares*



77 *Euthauma*

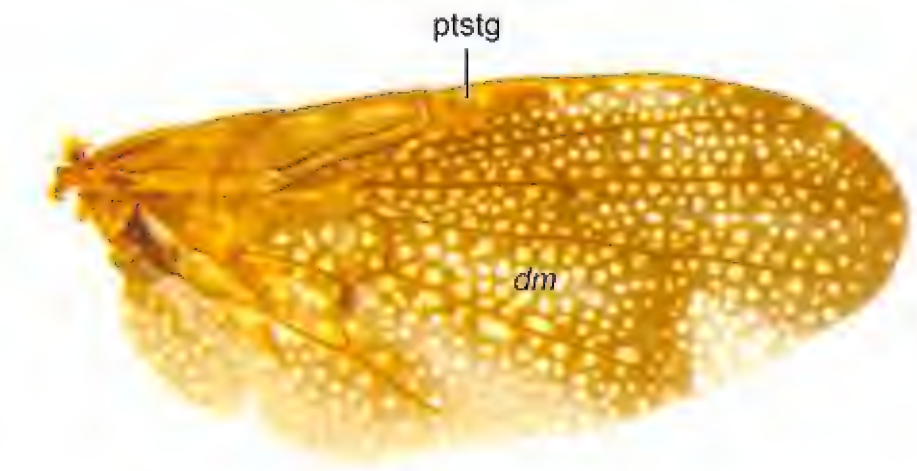


78 *Oedaspis* ♀



79 *Oedaspis*

80 *Perirhithrum*



81 *Tarchonanthea*

Figs 71.76–81. Wings of Tephritidae (dorsal views): (76) *Procecidochares utilis* Stone; (77) *Euthauma ghentianum* Munro; (78) *Oedaspis reticulata* Freidberg & Kaplan ♀; (79) *O. trapezoidalis* Munro; (80) *Perirhithrum marshalli* Bezzi; (81) *Tarchonanthea frauenfeldi* (Schiner).

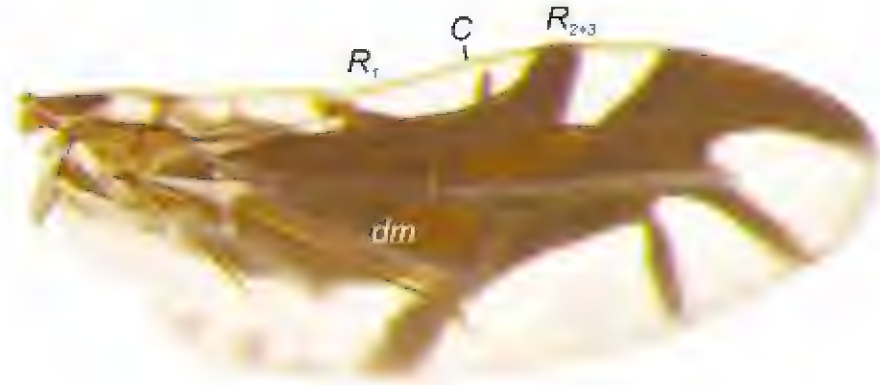
Abbreviations: *bm* – basal medial cell; *c* – costal cell; *C* – costal vein; *cua* – anterior cubital cell; *dm* – discal medial cell; m_1 – first medial cell; ptstg – pterostigma; R_1 – anterior branch of radius; r_1 – first radial cell; r_{4+5} – fourth + fifth radial cells; *Sc* – subcostal vein.

unknown. De Meyer (2006) provided a list of host-plants and an identification key to species.

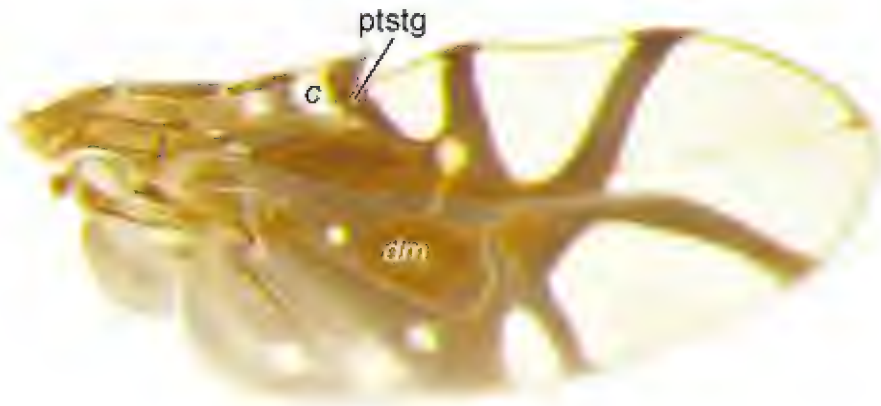
***Celidodacus* Hendel** (Trypetinae: Adramini)**.** An endemic genus of four described species, *C. coloniarum* Speiser, 1915 and *C. obnubilus* (Karsch, 1887) from East, Southern and West Africa, *C. madagascariensis* Hering, 1956 from Madagascar and *C. zambeziensis* Hancock, 1986 from Zimbabwe. Larvae develop in the fruit of *Canavalia* (Fabaceae) (Copeland *et al.* 2005). Biology and immature stages otherwise remain unknown. Several other species were synonymised by Hancock (1986*a*), who also provided an identification key to species.

***Ceratitis* MacLeay** (Dacinae: Ceratitidini)**.** An Afrotropical genus of 103 described species with one, the highly polyphagous pest species *C.* (*C.*) *capitata*, adventive in the western Palaearctic, Central and South America, Hawaii, St Helena Is. and Australia. Six subgenera are recognised. Two, *C.* (*Acropteromma* Bezzi), with *C.* (*A.*) *munroanum* (Bezzi, 1926) (Fig. 49) from Kenya, South Africa and Zimbabwe and *C.* (*Hoplolophomyia* Bezzi), with *C.* (*H.*) *cristata* (Bezzi, 1920) (Fig. 52) from Kenya, are monotypic. *Ceratitis sensu stricto* comprises eight species, including: *C.* (*C.*) *capitata* (Fig. 51); *C.* (*C.*) *catoirii* Guérin-Méneville, 1843, from Mauritius, Réunion Is. and Rodrigues Is.; *C.* (*C.*) *malgassa* Munro, 1939 from Madagascar and Mauritius; and *C.* (*C.*) *manjakatompo* Hancock, 1984, from Madagascar. The subgenus *C.* (*Ceratalaspis* Hancock) contains 45 species, with *C.* (*C.*) *andronotobaka* Hancock, 1984 and *C.* (*C.*) *sucini* De Meyer, 1998, restricted to Madagascar. The widespread *C.* (*C.*) *cosyra* (Walker, 1849) (Figs 2, 50) and *C.* (*C.*) *quinaria* (Bezzi, 1918) also occur in Madagascar and Yemen, respectively. The holotype of *C.* (*Ceratitis*) *capitata* is believed to

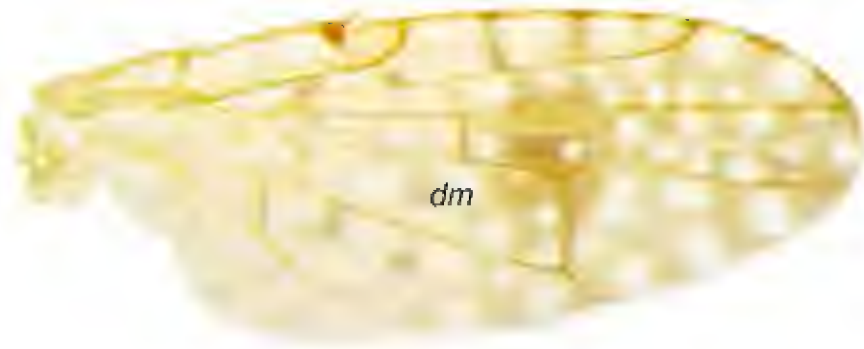
82 *Bactropota*



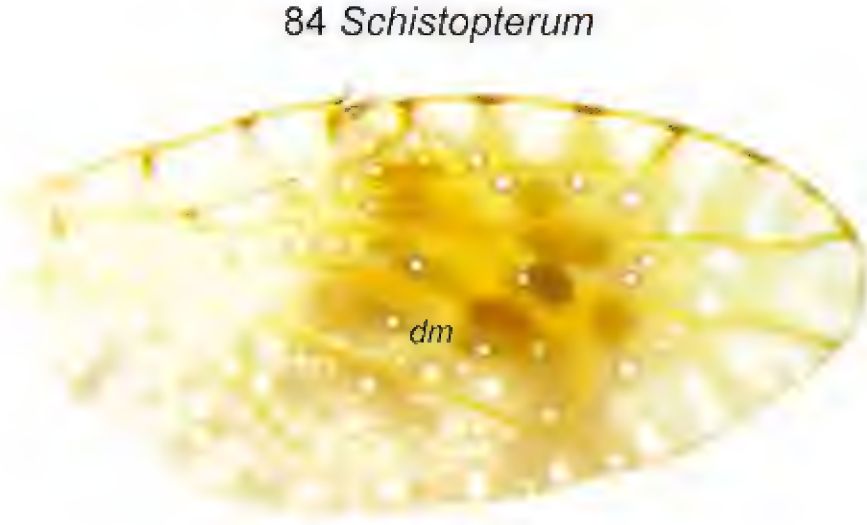
83 *Brachiopterna*



84 *Schistopterum*



85 *Clematochaeta*



86 *Cordylopteryx*

87 *Eutretosoma*

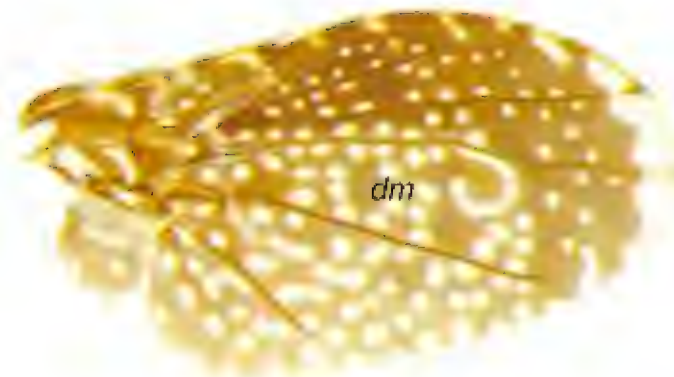
Figs 71.82–87. Wings of Tephritidae (dorsal views): (82) *Bactropota woodi* Bezzi; (83) *Brachiopterna katonae* Bezzi; (84) *Schistopterum* sp.; (85) *Clematochaeta perpallida* (Bezzi); (86) *Cordylopteryx marshalli* (Bezzi); (87) *Eutretosoma oculatum* (Hendel).

Abbreviations: *c* – costal cell; *C* – costal vein; *dm* – discal medial cell; ptstg – pterostigma; R_1 – anterior branch of radius; R_{2+3} – second branch of radius.

have originated in East Africa, not India as previously assumed (Hancock 2007*a*). The subgenus *C.* (*Pardalaspis* Bezzi) (Fig. 53) includes 11 species distributed in East, Southern and West Africa. The subgenus *C.* (*Pterandrus* Bezzi) comprises 37 species, including *C.* (*P.*) *argenteostriata* De Meyer & Freidberg, 2006 and *C.* (*P.*) *tananarivana* Hancock, 1984 from Madagascar. The East and Southern African pest species *C.* (*P.*) *quilicii* De Meyer, Mwatawala & Virgilio, 2016 (formerly confused with *C.* (*P.*) *rosa* Karsch, 1887 (Fig. 54): see De Meyer *et al*. 2015, 2016), is adventive in Mauritius and Réunion Is., while the widespread *C.* (*P.*) *pedestris* (Bezzi, 1924) also occurs in Madagascar. Larvae develop in fleshy fruits and many species are polyphagous. De Meyer *et al*. (2002) provided a host list for the genus. Males of possibly all species respond to the attractant terpinyl acetate; in addition, males of the subgenera *Ceratitis sensu stricto* and *C.* (*Pterandrus*) respond to trimedlure, while males of the subgenus *C.* (*Pardalaspis*) respond to methyl eugenol. Descriptions of the third-instar larvae of several economically important species were provided by Steck & Ekesi (2015). Phylogenetic relationships were discussed by De Meyer (2005). A gynandromorph *C.* (*C.*) *capitata*, with male head and female abdomen, was discussed and illustrated by Hancock (1980). Identification keys to species were provided by De Meyer (1996, 1998*a*: *C.* (*Pardalaspis*)), De Meyer (1998*b*: *C.* (*Ceratalaspis*)), De Meyer (2000: *Ceratitis sensu stricto*) and De Meyer & Freidberg (2006: *C.* (*Pterandrus*)). The subgenera *C.* (*Acropteromma*) and *C.* (*Hoplolophomyia*) were reviewed and several species of *C.* (*Ceratalaspis*), *C.* (*Pardalaspis*) and *C.* (*Pterandrus*) subsequently added by De Meyer & Copeland (2001, 2005, 2009) and De Meyer *et al*. (2016). Most of the pest species were treated by White & Elson-Harris (1992) and most of the Indian Ocean island endemics were illustrated by Hancock (1984).

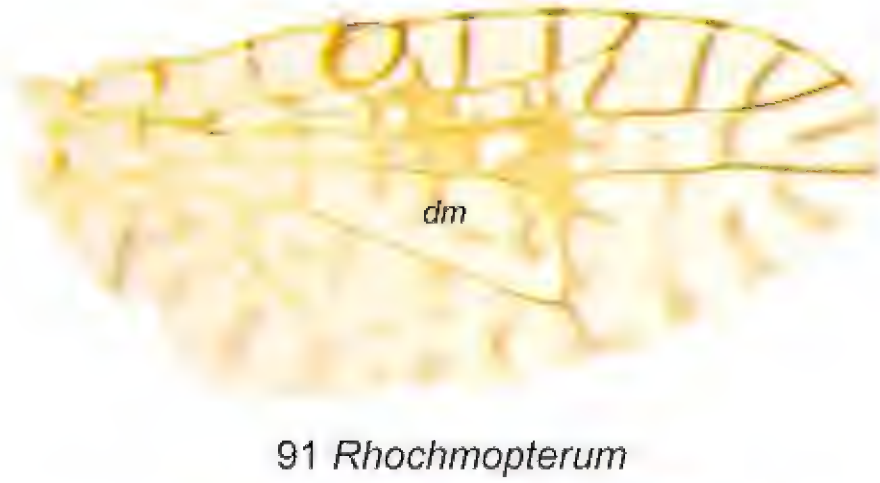
***Ceratitoides* Hendel** (Dacinae: Gastrozonini)**.** An endemic monotypic genus, with the single described species, *C. nigromaculatus* Hendel, 1928 (Figs 6, 64, 183), recorded from

88 *Melanopterella*

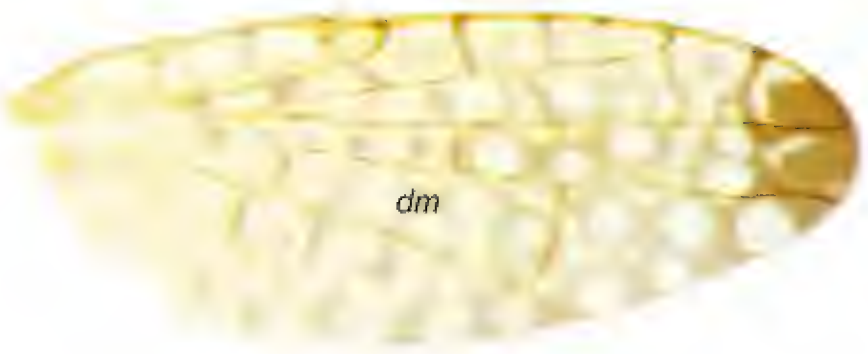


89 *Microtreta*

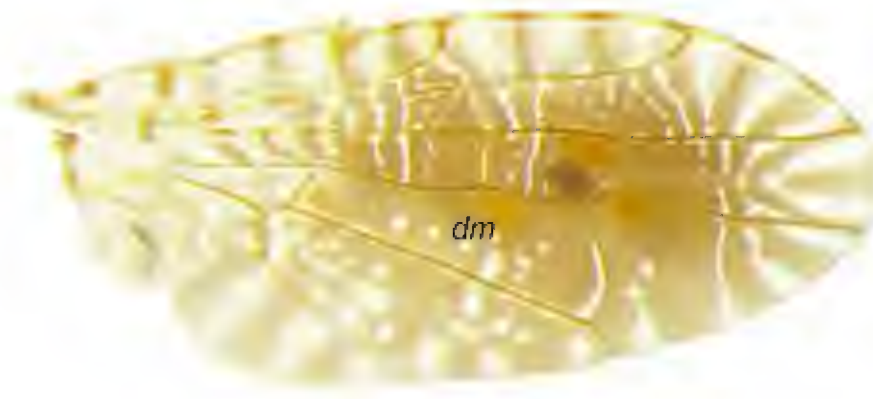
90 *Rhabdochaeta*



91 *Rhochmopterum*



92 *Schistotephritis*



93 *Setoides*

Figs 71.88–93. Wings of Tephritidae (dorsal views): (88) *Melanopterella nigra* (Bezzi); (89) *Microtreta fini* Freidberg; (90) *Rhabdochaeta mucronata* Hering; (91) *Rhochmopterum neuropteripenne* Speiser; (92) *Schistotephritis acrophthalma* (Bezzi); (93) *Setoides mirabilis* Zonstein & Freidberg.

Abbreviations: *dm* – discal medial cell; r_1 – first radial cell.

Cameroon and Uganda. It was referred to the Gastrozonini by Kovac *et al*. (2006) and larvae possibly develop in the shoots of bamboo. Biology and immature stages of the species otherwise remain unknown. It differs from other Afrotropical Gastrozonini in abdominal shape, appearing closest to the Oriental genus *Pardalaspinus* Hering.

***Chipingomyia* Hancock** (Tephritinae: Pliomelaenini)**.** An endemic genus of two described species, *C. manica* Hancock, 1986 (Figs 11, 133, 134) from Tanzania and Zimbabwe and *C. nigrapex* (Munro, 1937) from South Africa. Of uncertain placement, it is provisionally referred here to the Pliomelaenini, based on a molecular similarity to *Bezzina*. The sexes are dimorphic in wing pattern and the two species are possibly synonymous. Biology and immature stages remain unknown. No identification key to species is currently available.

***Clematochaeta* Hering** (Tephritinae: Schistopterini)**.** An endemic genus of five described (Fig. 85) and at least 20 undescribed species from throughout the continental Afrotropics and Madagascar, including three illustrated by Hancock (1986*b*): two as *Rhochmopterum* spp. B & C (= *Clematochaeta* spp. nov. 1 & 2 in Hancock 2003*b*), from Malawi and Zimbabwe or Uganda and Zimbabwe respectively, plus *Clematochaeta* sp. from Malawi and Zambia. Larvae develop in flower heads of *Vernonia* (Asteraceae). Biology and immature stages otherwise remain unknown. No identification key to species is currently available.

***Clinotaenia* Bezzi** (Dacinae: Gastrozonini)**.** An endemic genus of six described species (Fig. 66) distributed in East, Southern and West Africa. It was referred to Gastrozonini by Kovac *et al*. (2006) and appears to be related to *Bistrispinaria*. The genus is probably associated with Poaceae. Biology and immature stages otherwise remain unknown. Hancock (1999) provided an identification key to five species, to which should be added *C. angusticeps* (Bezzi, 1923) from Burundi, Chad and Democratic Republic of Congo, transferred from *Carpophthoromyia* by De Meyer (2006).

***Coelopacidia* Enderlein** (Trypetinae: Adramini)**.** A genus of nine described Afrotropical (Fig. 25) and one undescribed Oriental species. Most species are distributed in East, Southern and West Africa, but one species, *C. madagascariensis* Enderlein, 1911, is confined to Madagascar. Larvae tunnel in the stems of *Cineraria* (Asteraceae), *Polemannia* (Apiaceae) and *Senecio* (Asteraceae) and pupariate within the stem (Munro 1926). Biology and immature stages otherwise remain unknown. Hancock (2019) provided an identification key to species.

***Coelotrypes* Bezzi** (Trypetinae: Adramini)**.** A genus of 19 described species, 12 Afrotropical (Figs 26, 27) and seven Oriental and Australasian. Most Afrotropical species are distributed in East, Southern and West Africa, but *C. hammersteini* Enderlein, 1911, is confined to Madagascar. The widespread *C. vittatus* Bezzi, 1923 (Fig. 28) also occurs in Madagascar and (as subsp. *C. v. setiger* Hering, 1958) in Cabo Verde. Two undescribed species are known from Kenya (Copeland *et al*. 2005). Larvae develop in the flower buds of *Ipomoea* (Convolvulaceae). Biology and immature stages otherwise remain unknown. Hancock (1986*a*) provided an identification key to the described Afrotropical species.

***Conradtina* Enderlein** (Trypetinae: Adramini)**.** An endemic genus of three described species: *C. acroleuca* Speiser, 1913, recorded from Angola, Cameroon, Kenya, Sierra Leone and Zimbabwe; *C. longicornis* Enderlein, 1911 (Fig. 29), from Cameroon, Democratic Republic of Congo, Equatorial Guinea and Nigeria; and *C. suspensa* Bezzi, 1918, from Democratic Republic of Congo and Uganda, plus an undescribed species from Madagascar. Biology and immature stages remain unknown. Several other species were synonymised by Hancock (1986*a*), who also provided an identification key to described species.

***Cordylopteryx* Hering** (Tephritinae: Schistopterini)**.** An endemic genus of three described species distributed in Southern Africa: *C. lesneae* (Séguy, 1933), from Mozambique, Namibia and Zimbabwe; *C. marshalli* (Bezzi, 1924) (Fig. 86) from South Africa and Zimbabwe; and *C. neavei* (Bezzi, 1920), from Malawi, Namibia and Zimbabwe, plus at least nine undescribed species. Larvae develop in flower heads of *Vernonia* (Asteraceae). Biology and immature stages otherwise remain unknown. No identification key to species is currently available.

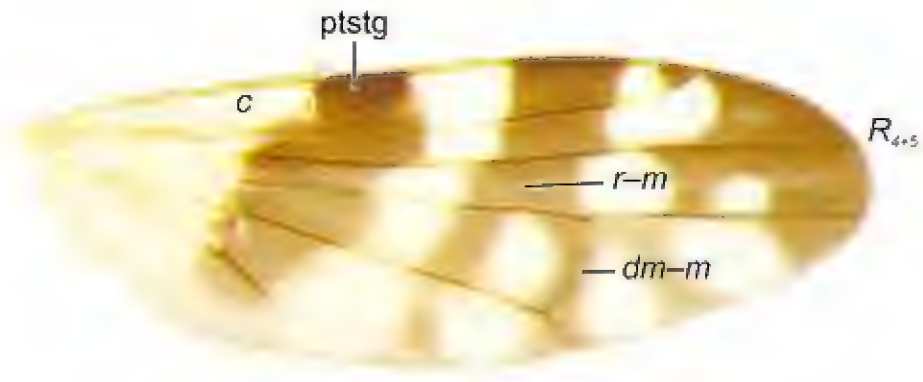
***Cosmetothrix* Munro** (Tephritinae: Eutretini)**.** An endemic monotypic genus, with the single described species, *C. discoidalis* (Bezzi, 1924) (Fig. 14), from South Africa. Larvae develop in twig galls on *Vernonia anisochaetoides* Sonder (Asteraceae). Biology and immature stages otherwise remain unknown.

***Craspedoxantha* Bezzi** (Tephritinae: Terelliini)**.** A genus of two Oriental and nine described Afrotropical species, occurring in the continental Afrotropics as far north as Sudan. An undescribed species (Fig. 69) is known from Ethiopia. Larvae develop in flower heads (and sometimes adjacent stems) of several genera of Asteraceae. Biology and immature stages otherwise remain unknown. Freidberg (1985) provided an identification key to the nine species then known, with two additional species and revised phylogenies provided subsequently by Freidberg & Mathis (1990) and Freidberg (1999).

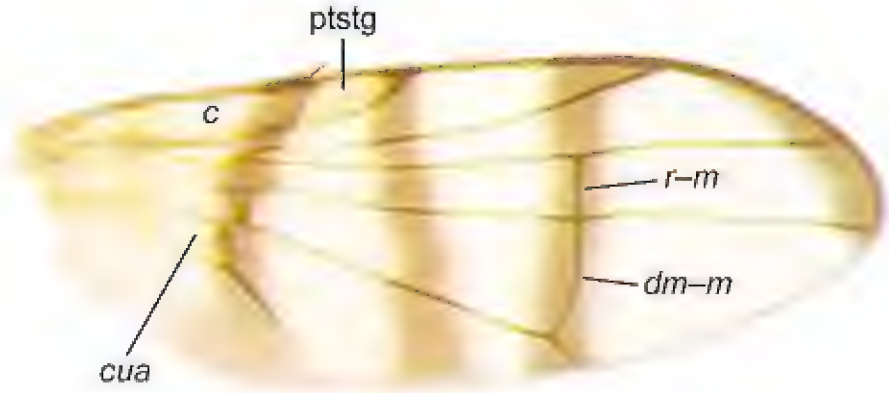
***Cryptophorellia* Freidberg & Hancock** (Tephritinae: Axiothaumini)**.** An endemic genus of 16 described species (Fig. 75), including 10 distributed in East, Southern and West Africa and six from Madagascar. Two undescribed species occur in Ethiopia and Tanzania, respectively. Wing shape and pattern, particularly in the Madagascan species, are often sexually dimorphic. Larvae develop in the flower heads of *Crassocephalum* and *Senecio* (Asteraceae) and appear to pupariate in the soil. Freidberg & Hancock (1989) provided descriptions of the larva and puparium and an identification key to species.

***Dacus* F.** (Dacinae: Dacini)**.** A genus of *ca* 270 species occurring in the Afrotropical, Australasian and Oriental Regions. The *ca* 195 Afrotropical species were referred to seven subgenera by White (2006) and eight by Hancock & Drew (2006), subsequently reduced to seven by Hancock (2009), with the synonymy of *D.* (*Metidacus* Munro) with *D.* (*Leptoxyda* Macquart). The 37 genera recognised by Munro (1984) are now regarded as no more than subgenera or species-groups. Some re-assignments of species within the subgenera were made by Hancock (2009, 2010*b*), based on further information. For habitus illustrations of 12 species see Hancock (2003*b*). Within the Afrotropics, the largely Australasian and Oriental subgenus *D.* (*Neodacus* Perkins)

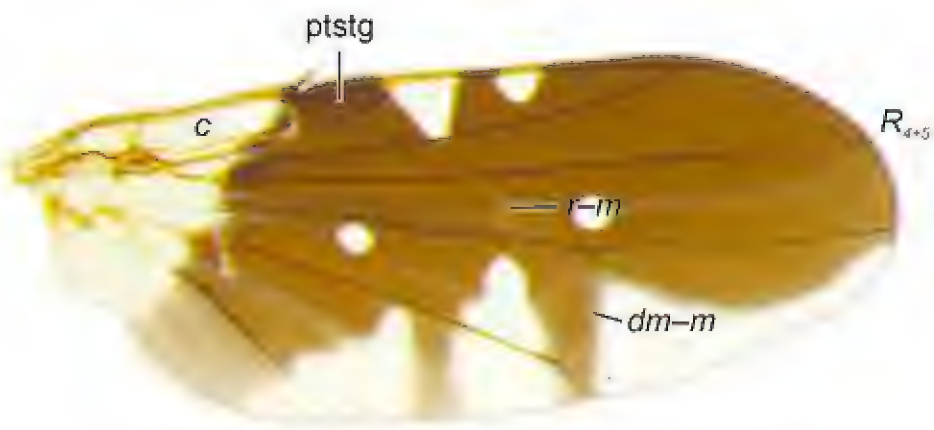
is represented by three endemic species in Madagascar. The subgenera *D.* (*Didacus* Collart) and *D.* (*Leptoxyda* Macquart) are also represented in the Oriental Region, while *Dacus sensu stricto*, *D.* (*Lophodacus* Collart), *D.* (*Mictodacus* Munro) and *D.* (*Psilodacus* Collart), are endemic to the Afrotropics. Some 14 species, including the otherwise non-Afrotropical *D.* (*Leptoxyda*) *persicus* Hendel, 1927, are known from the Arabian Peninsula. Larvae develop in the fruit or flowers of Cucurbitaceae and Passifloraceae (*Dacus sensu stricto*, *D.* (*Didacus*), *D.* (*Lophodacus*) and *D.* (*Mictodacus*)), or the pods primarily of Apocynaceae: Asclepiadoideae (*D.* (*Leptoxyda*), *D.* (*Neodacus*) and *D.* (*Psilodacus*)). Significant pests of cucurbits include *D.* (*Dacus*) *bivittatus, D.* (*Didacus*) *ciliatus* (Loew, 1862) and *D.* (*Didacus*) *vertebratus* Bezzi, 1908 (Fig. 1). Partial descriptions of some third-instar larvae were provided by White & Elson-Harris (1992: 331). Males of many species, particularly in the subgenera *Dacus sensu stricto*, *D.* (*Didacus*), *D.* (*Mictodacus*) and *D.* (*Neodacus*), respond to the male attractant cue-lure and one, *D.* (*Didacus*) *vertebratus* (Fig. 1), responds to vert-lure. No attractant has been recorded for *D.* (*Didacus*) *ciliatus*. Species in the subgenus *Dacus sensu stricto* appear to prefer forest and moist woodland environments, while those in the other subgenera prefer open woodland habitats. Both sexes of many species are known to form communal roosts, particularly during colder weather (Hancock 1989: 54). White (2006) provided an identification key to Afrotropical species known at that time, but additional species have been described subsequently by White & Goodger (2009) and De Meyer *et al.* (2013); from the latter, *D. goergeni* De Meyer, White & Goodger, 2013, should be transferred from the subgenus *D.* (*Psilodacus*) to the subgenus *D.* (*Leptoxyda*).



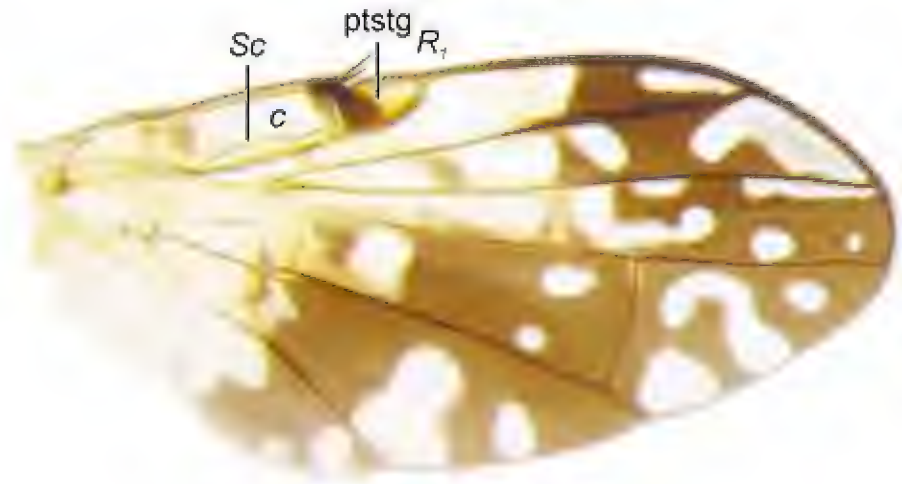
94 *Afraciura*



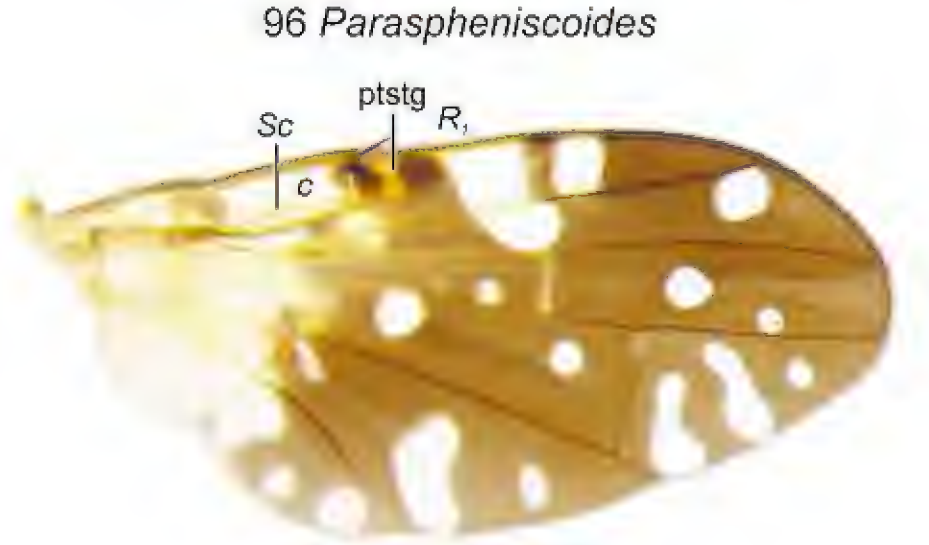
95 *Munroella*



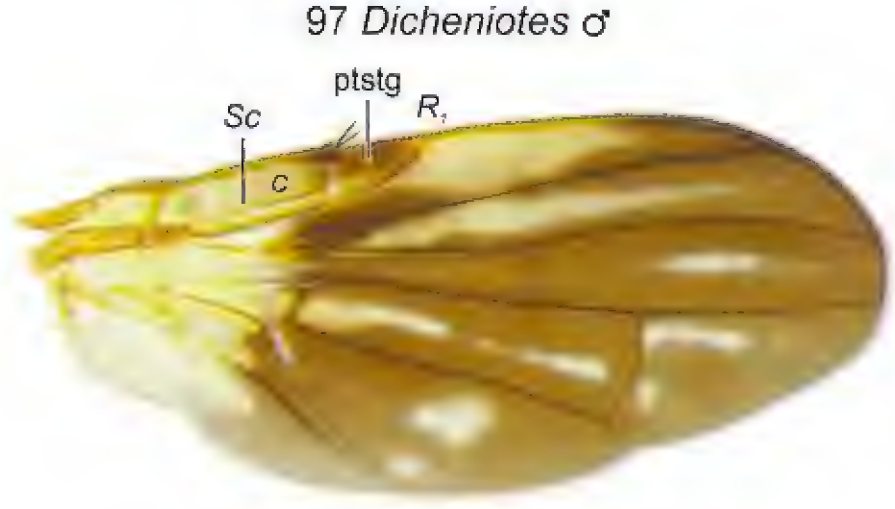
96 *Parasphenioscoides*



97 *Dicheniotes* ♂



98 *Dicheniotes* ♀



99 *Dicheniotes* ♂

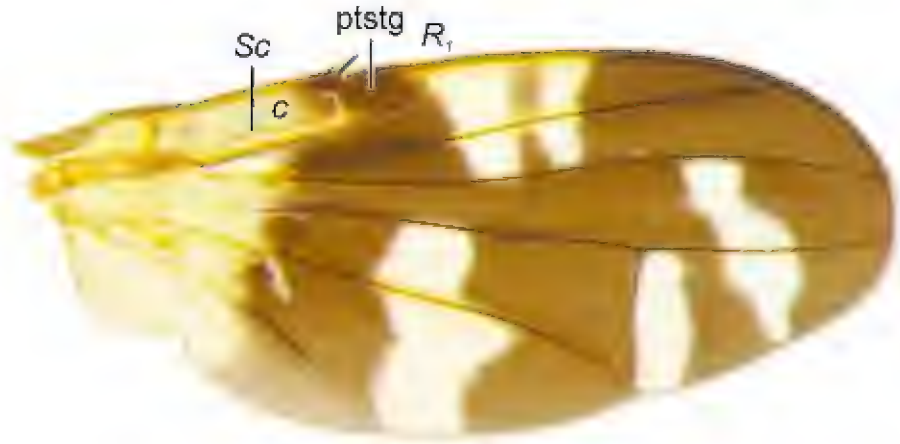
Figs 71.94–99. Wings of Tephritidae (dorsal views): (94) *Afraciura zernyi* Hering; (95) *Munroella myiopitina* Bezzi; (96) *Parasphenioscoides binarius* (Loew); (97) *Dicheniotes polyspila* (Bezzi) ♂; (98) same ♀; (99) *D. tephronotus* (Bezzi) ♂.

Abbreviations: *c* – costal cell; *cua* – anterior cubital cell; *dm–m* – discal medial crossvein; ptstg – pterostigma; R_1 – anterior branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Sc* – subcostal vein.

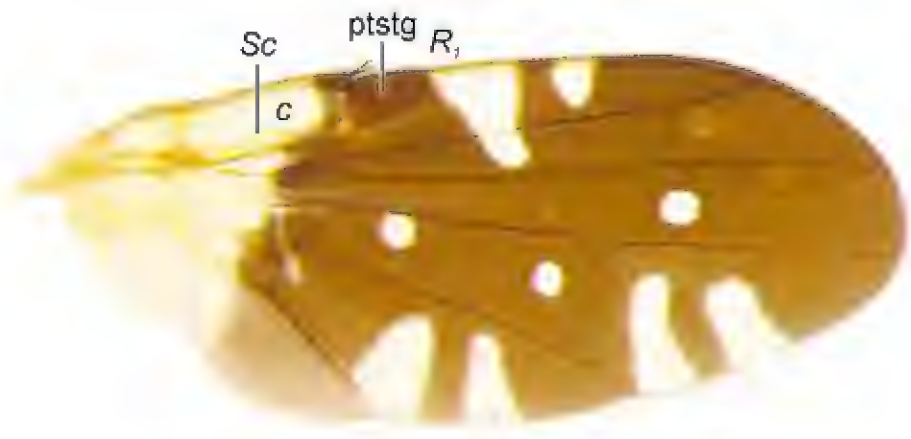
***Dectodesis* Munro** (Tephritinae: Tephritini)**.** An endemic genus of 14 described species (Fig. 163), including: *D. comis* (Munro, 1954) and *D. spatiosa* Munro, 1954 from Madagascar, plus *D. auguralis* (Bezzi, 1908) from Eritrea to Zimbabwe, Saudi Arabia and Yemen. An undescribed species is also known from Kenya (Copeland *et al*. 2005) and four others from Madagascar. Larvae develop in flower heads of *Erigeron*, *Gnaphalium* and *Helichrysum* (Asteraceae: Inuleae). Biology and immature stages otherwise remain unknown. No identification key to species is currently available.

***Desmella* Munro** (Tephritinae: Tephritini)**.** A genus of five described species, two restricted to Palaearctic North Africa and three Afrotropical species: *D. anceps* (Loew, 1861) (Fig. 136), from Lesotho, Namibia and South Africa; *D. clarinetta* (Munro, 1939), from Namibia and South Africa; and *D. myiopitoides* (Bezzi, 1908), possibly a species complex, from northeast, East and Southern Africa, Madagascar and possibly Saudi Arabia and Oman (Merz & Dawah 2005). Larvae develop in flower heads of *Chrysocoma* (Asteraceae). Biology and immature stages otherwise remain unknown. No identification key to species is currently available, but Munro (1957*a*) reviewed and illustrated the Afrotropical species.

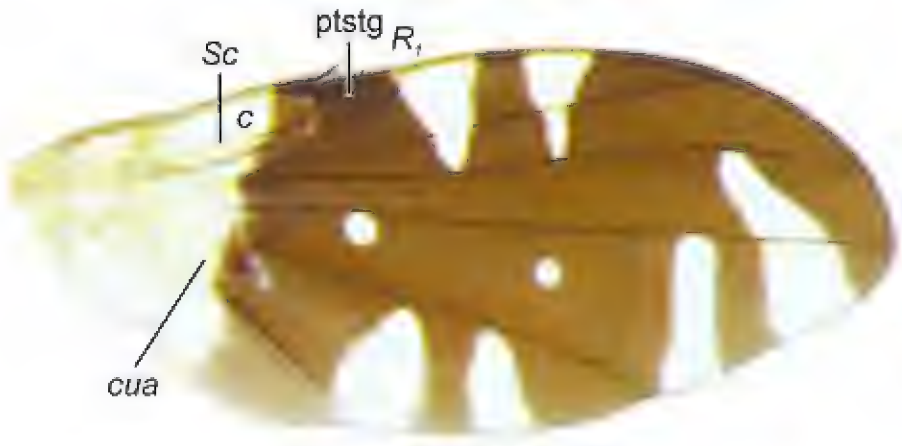
***Deroparia* Munro** (Tephritinae: Pliomelaenini)**.** An endemic monotypic genus, with the single species, *D. reticulata* (Munro, 1929), described from western Namibia. Based on morphological evidence, it appears to be most closely related to



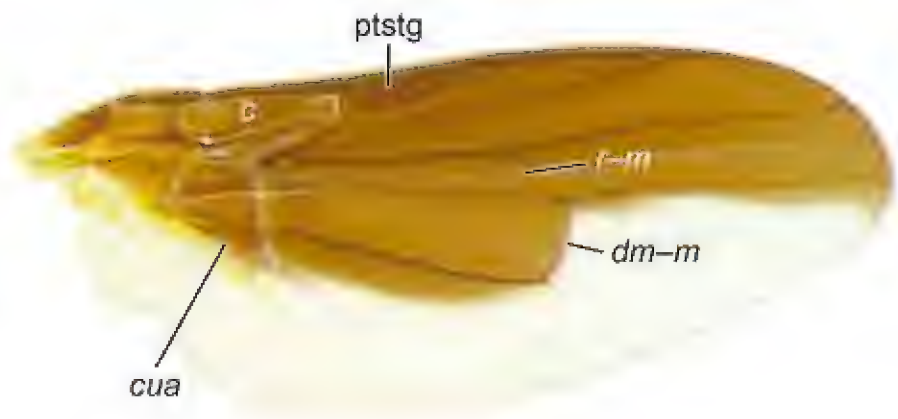
100 *Dicheniotes* ♀



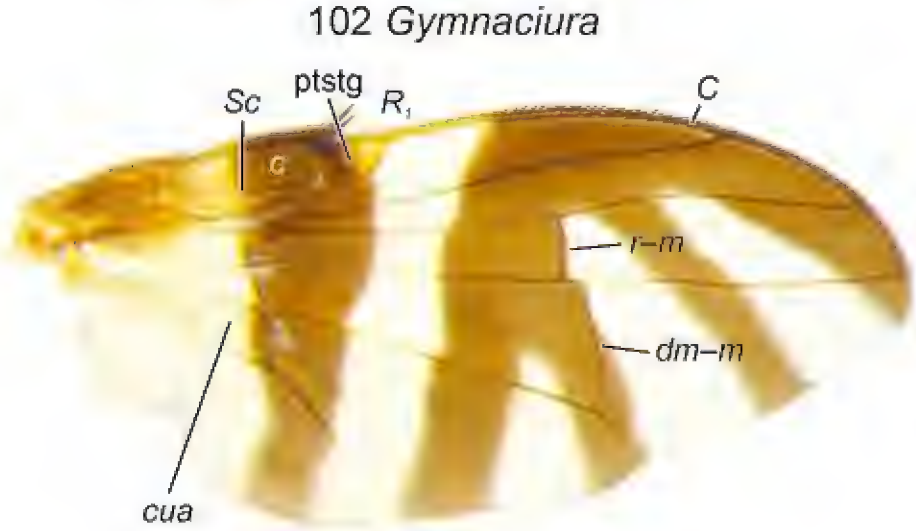
101 *Dicheniotes*



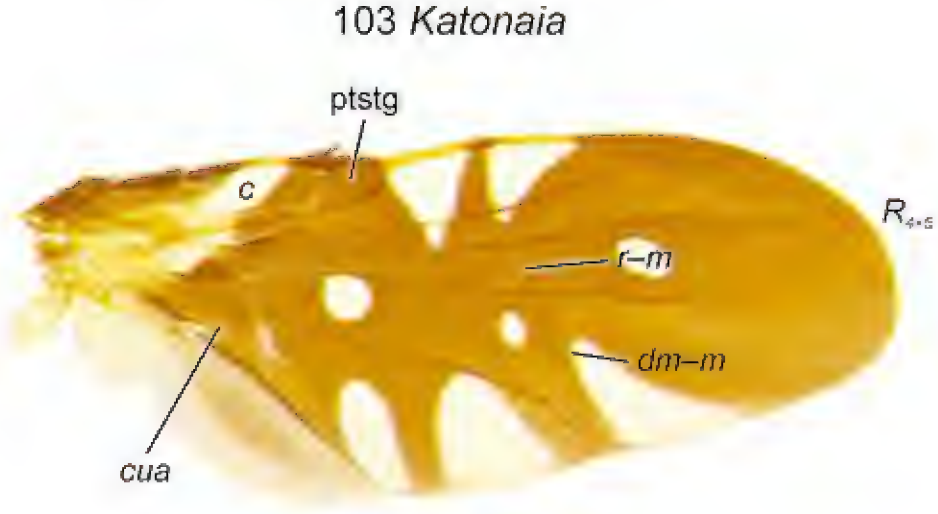
102 *Gymnaciura*



103 *Katonaia*



104 *Oedoncus*



105 *Oxyaciura*

Figs 71.100–105. Wings of Tephritidae (dorsal views): (100) *Dicheniotes tephronotus* (Bezzi) ♀; (101) *D. enzoria* (Munro); (102) *Gymnaciura austeni* (Munro); (103) *Katonaia arushae* Munro; (104) *Oedoncus taenipalpis* Speiser; (105) *Oxyaciura tibialis* (Robineau-Desvoidy).

Abbreviations: *c* – costal cell; *C* – costal vein; *cua* – anterior cubital cell; *dm–m* – discal medial crossvein; ptstg – pterostigma; R_1 – anterior branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Sc* – subcostal vein.

Euryphalara and *Xenodorella* (Hancock 2000). Biology and immature stages remain unknown.

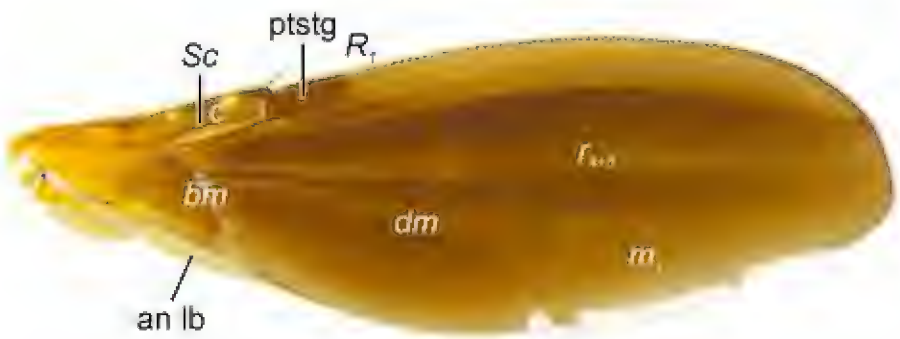
***Dicheniotes* Munro** (Tephritinae: Tephrellini)**.** An endemic genus of 19 described species, distributed in north-east, East and Southern Africa, with three species also reaching the Arabian Peninsula and one, *D. sokotrensis* (Hering, 1939), recorded only from Socotra Is. (Yemen). An additional undescribed species is known from Madagascar. Some species are sexually dimorphic in wing pattern (Figs 97–100), while others are monomorphic (Fig. 101). Larvae develop in flower heads of Lamiaceae and in Kenya *D. aeneus* (Munro, 1947) was reared from *Pycnostachys meyeri* Gürke. Biology and immature stages otherwise remain unknown. Hancock (2012) provided an identification key to species, many transferred from *Pediapelta*.

***Dioxyna* Frey** (Tephritinae: Tephritini)**.** A genus of 11 described species occurring in all zoogeographical regions except Antarctica. Only the widespread Old World species *D. sororcula* (Wiedemann, 1830) occurs in the Afrotropics, being recorded from north-east, East and Southern Africa, Madagascar, Réunion Is., Seychelles, Saudi Arabia and Yemen. Larvae develop in flower heads of Asteraceae, particularly *Bidens*. Biology and immature stages otherwise remain unknown. Synonymised with *Campiglossa* on molecular evidence by Han & Ro (2019), but kept separate here, pending investigation of other related genera in the *Campiglossa*-group.

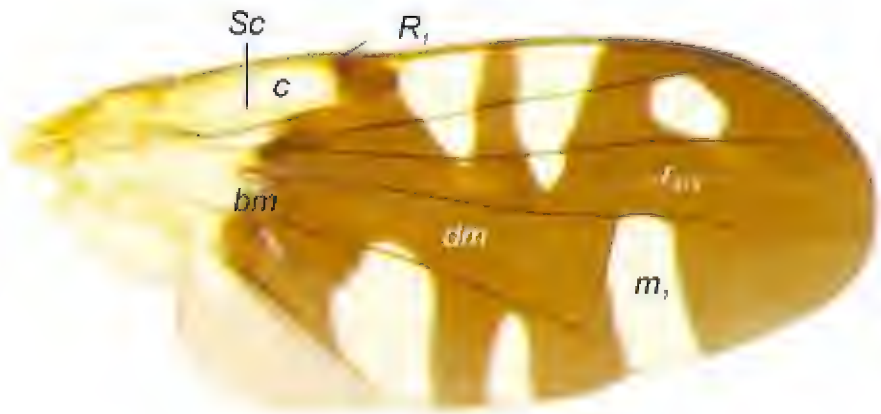
***Dorycricus* Munro** (Tephritinae: Tephrellini)**.** An endemic monotypic genus, with the single described species, *D. ruater* Munro, 1947 (Fig. 108), from Kenya. Biology and immature stages remain unknown.

106 *Ypsilomena*

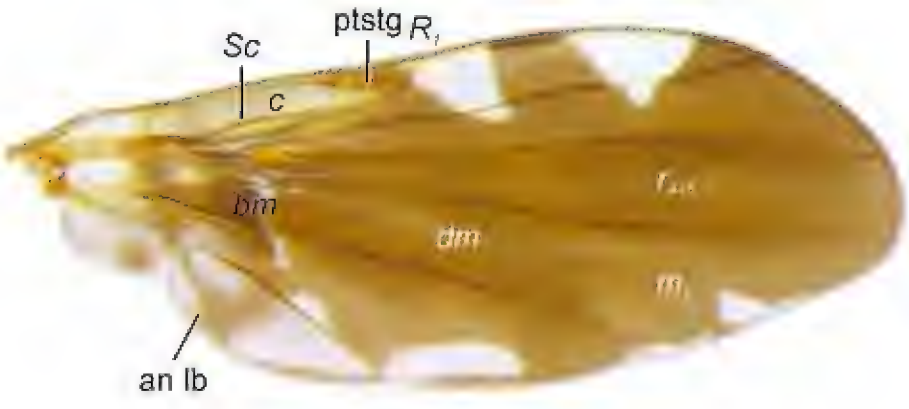
107 *Brachyaciura*



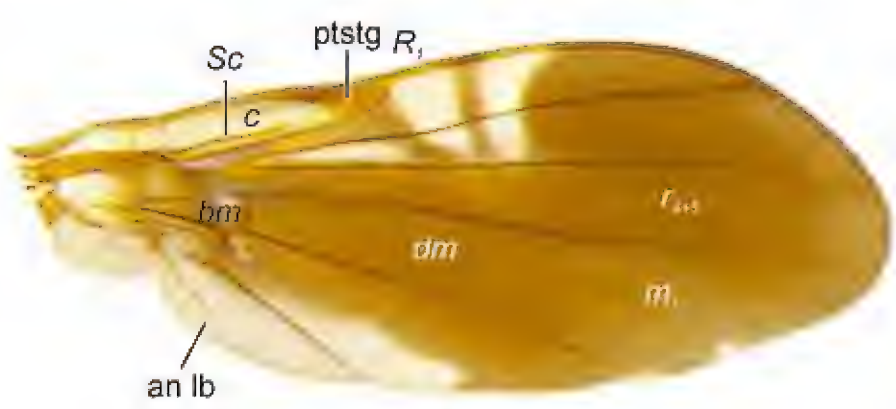
108 *Dorycricus*



109 *Metasphenisca*



110 *Ocnerioxyna* ♂



111 *Ocnerioxyna* ♀

Figs 71.106–111. Wings of Tephritidae (dorsal views): (106) *Ypsilomena compacta* (Bezzi); (107) *Brachyaciura kovacsi* Bezzi; (108) *Dorycricus ruater* Munro; (109) *Metasphenisca gracilipes* (Loew); (110) *Ocnerioxyna maripilosa* (Munro) ♂; (111) same ♀.

Abbreviations: an lb – anal lobe; *bm* – basal medial cell; *c* – costal cell; *cua* – anterior cubital cell; *dm* – discal medial cell; m_1 – first medial cell; ptstg – pterostigma; R_1 – anterior branch of radius; r_{4+5} – fourth + fifth radial cells; *Sc* – subcostal vein.

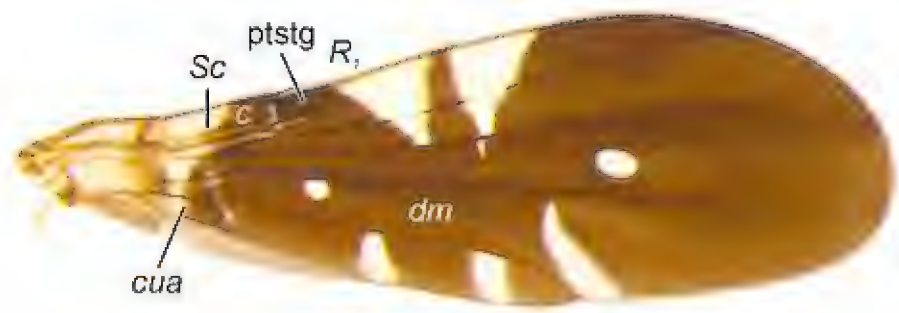
***Elaphromyia* Bigot** (Tephritinae: Pliomelaenini)**.** A genus of nine described species occurring in the Afrotropical, Australasian and Oriental Regions. Four species occur in the Afrotropics: *E. adatha* (Walker, 1849) (Fig. 115), recorded from Botswana, Democratic Republic of Congo, Mozambique, South Africa and Zimbabwe; *E. fissa* Munro, 1957, described from South Africa; *E. pallida* Bezzi, 1926, recorded from Ethiopia, Kenya and South Africa; plus *E. pterocallaeformis* (Bezzi, 1913), an Oriental species also recorded from Yemen in the Afrotropical part of the Arabian Peninsula. An additional undescribed species is known from Ethiopia, Kenya and Uganda. Larvae develop in flower heads of several genera of Acanthaceae. Biology and immature stages otherwise remain unknown. Munro (1947) provided an identification key to all Afrotropical species except the subsequently described *E. fissa*.

***Elgonina* Munro** (Tephritinae: Tephritini)**.** An endemic genus of 14 described species (Fig. 145) known from highlands in north-east, East and Southern Africa, with a possibly undescribed species known from Cameroon. Larvae develop in flower heads of *Conyza* and *Microglossa* (Asteraceae). Biology and immature stages otherwise remain unknown. Freidberg & Merz (2006) provided an identification key to species.

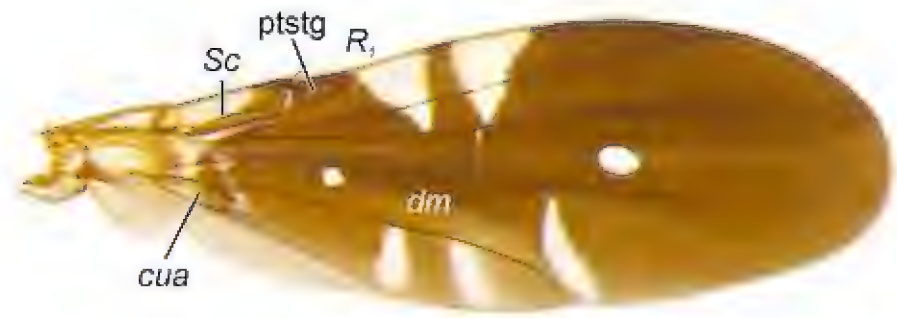
***Ensina* Robineau-Desvoidy** (Tephritinae: Noeetini)**.** A genus of six described species occurring in the Afrotropical, Neotropical and Palaearctic Regions. One Palaearctic species, *E. sonchi* (L., 1767), extends into, or introduced to, several other countries, including Ethiopia in the Afrotropics. Larvae develop in flower heads of many genera of Asteraceae: Cichoroideae. Biology and immature stages otherwise remain unknown. No identification key to species is currently available.

***Euaresta* Loew** (Tephritinae: Tephritini)**.** A New World genus of 15 described species occurring primarily in the Nearctic and Neotropical Regions. One species, the Neotropical *E. bullans*

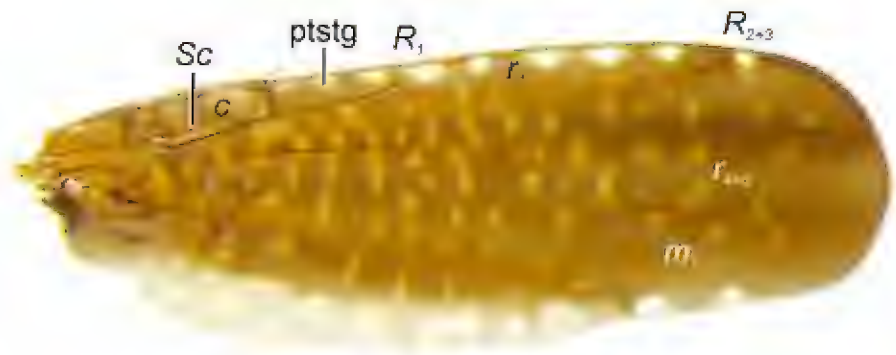
112 *Tephraciura*



113 *Paraciura*



114 *Paraciura*



115 *Elaphromyia*

116 *Ghentia*

117 *Hyaloctoides*

Figs 71.112–117. Wings of Tephritidae (dorsal views): (112) *Tephraciura oborinia* (Walker); (113) *Paraciura perpicillaris* (Bezzi); (114) same; (115) *Elaphromyia adatha* (Walker); (116) *Ghentia millepunctata* (Bezzi); (117) *Hyaloctoides semiater* (Loew).

Abbreviations: *c* – costal cell; *C* – costal vein; *cua* – anterior cubital cell; *dm* – discal medial cell; M_1 – first branch of media; m_1 – first medial cell; ptstg – pterostigma; R_1 – anterior branch of radius; r_1 – first radial cell; r_{2+3} – second + third radial cell; R_{2+3} – second branch of radius; r_{4+5} – fourth + fifth radial cells; R_{4+5} – third branch of radius; *Sc* – subcostal vein.

(Wiedemann, 1830) (Fig. 143), was accidentally introduced into many countries, including South Africa. Larvae develop in seeds of *Xanthium spinosum* L. (Asteraceae). Biology and immature stages otherwise remain unknown. No identification key to species is currently available.

***Euarestella* Hendel** (Tephritinae: Tephritini)**.** A genus of five described and one undescribed species, occurring in the Afrotropical and Palaearctic Regions. Three species occur in the Afrotropics: *E. iphionae* (Efflatoun, 1924), recorded from Egypt and Sudan to Saudi Arabia and Iran; *E. vanharteni* Mertz, 2008, from United Arab Emirates; plus an undescribed species from United Arab Emirates (Merz 2008). A further species, *E. abyssinica* Hering, 1937 from Ethiopia, was regarded as probably not congeneric by Merz (1999: 644) and *Actinoptera vinsoni* Munro from Mauritius also runs here in the above identification key. Larvae develop in flower heads or stem galls of *Helichrysum*, *Iphiona* and *Pulicaria* (Asteraceae: Inuleae). Immature stages of *E. iphionae* were described by Efflatoun (1927). Merz (2008) provided an identification key to species.

***Eumictoxenus* Munro** (Dacinae: Ceratitidini)**.** An endemic monotypic genus, with the single described species, *E. leleupi* Munro, 1962 (Fig. 55), from Tanzania, although an undescribed species from Nyika Plateau, north-east Zambia, possibly belongs in this genus. Biology and immature stages remain unknown.

***Euryphalara* Munro** (Tephritinae: Pliomelaenini)**.** An endemic genus of three described species: *E. barnardi* (Bezzi, 1924), from western Namibia; *E. extensa* Munro, 1938, from northern South Africa; and *E. mecistocephala* (Munro, 1929) from western Namibia, plus an additional undescribed species from western Namibia. Larval host-plants not confirmed, but adults have been swept from *Monechma* (Acanthaceae) and this is the likely host-plant. Biology and immature stages otherwise remain unknown. Hancock (2000) provided an identification key to species that also included the monotypic *Deroparia* and *Xenodorella*.

***Euthauma* Munro** (Tephritinae: Dithrycini: Platensinina)**.** An endemic monotypic genus, with the single described species, *E. ghentianum* Munro, 1949 (Fig. 77), from South Africa. Larvae form stem galls on *Schistostephium heptalobium* Benth. (Asteraceae). Biology and immature stages otherwise remain unknown. *Euthauma* was referred to the subtribe Platensinina by Hancock (2001).

***Eutretosoma* Hendel** (Tephritinae: Schistopterini)**.** An endemic genus of four described species (Fig. 87) distributed from Ethiopia to Southern Africa and 13 undescribed species, including one each from Madagascar (with distinct apical rays) and Aldabra Is. (Seychelles). Larvae develop in flower heads of *Triptocephalum* and *Vernonia* (Asteraceae). Biology and immature stages otherwise remain unknown. No identification key to species is currently available.

***Freidbergia* Merz** (Tephritinae: Tephritini)**.** An endemic monotypic genus, with the single described species, *F. mirabilis* Merz, 1999 (Fig. 164), recorded from Ethiopia to Malawi, Madagascar and Saudi Arabia. Larvae develop in flower heads of *Pluchea* (Asteraceae: Inuleae). Biology and immature stages otherwise remain unknown.

***Ghentia* Munro** (Tephritinae: Pliomelaenini)**.** An endemic monotypic genus, with the single described species, *G. millepunctata* (Bezzi, 1918) (Fig. 116), recorded from Eritrea, Tanzania and South Africa. Larvae develop in flower heads of *Lepidogathis* (Acanthaceae) and pupariate between the sepals. Biology and immature stages otherwise remain unknown.

***Goniurellia* Hendel** (Tephritinae: Tephritini)**.** A genus of 10 described species (Figs 165, 166) occurring in the Afrotropical, Oriental and Palaearctic Regions. Seven species occur in the Afrotropics, with six of these recorded from the Arabian Peninsula and Socotra Is. (Yemen). Larvae develop in flower heads of Asteraceae: Inuleae, particularly *Pallentis* and *Pulicaria*. Biology and immature stages otherwise remain unknown. Freidberg (1980) provided an identification key to species, modified by Merz (2002), to include additional species.

***Gymnaciura* Hering** (Tephritinae: Tephrellini)**.** An endemic genus of two described species: *G. austeni* (Munro, 1935) (Fig. 102), distributed over much of the continental Afrotropics, Madagascar, Saudi Arabia and Yemen; and *G. neavei* (Bezzi, 1920), recorded from Malawi and Zimbabwe. An additional undescribed species is known from Kenya (Copeland *et al*. 2005). Biology and immature stages remain unknown. Munro (1947) provided an identification key to described species (as *Tanaosema*).

***Gymnosagena* Munro** (Tephritinae: Tephritini)**.** An endemic genus of five described species (Fig. 145), distributed in the highlands of East and Southern Africa and in Madagascar. Larvae develop in flower heads of several genera of Asteraceae. Biology and immature stages otherwise remain unknown. Freidberg & Merz (2006) provided an identification key to species.

***Hemilea* Loew** (Trypetinae: Trypetini)**.** A genus of 29 described species occurring in the Afrotropical, Australasian, Oriental and Palaearctic Regions. One species, *H. malgassa* Hancock, 1985, is Afrotropical and is confined to Madagascar. Where known, larvae are leaf-miners. Biology and immature stages otherwise remain unknown. The Afrotropical species can be identified by reference to Hancock (1985*a*).

***Heringomyia* Hardy** (Tephritinae: Schistopterini)**.** An endemic monotypic genus, with the single described species, *H. fordiana* (Munro, 1935), recorded from Rwanda and Zimbabwe, but an additional three undescribed species are known. Larvae develop in flower heads of *Vernonia* (Asteraceae). Biology and immature stages otherwise remain unknown. The genus is in need of revision and no identification key to species is currently available.

***Hoplandromyia* Bezzi** (Trypetinae: Trypetini)**.** A genus of seven described species occurring in the Afrotropical and Oriental Regions. Five species occur in the Afrotropics, including *H. madagascariensis* Hancock, 1985 (Fig. 43) from Madagascar and *H. tetracera* Bezzi, 1923 from Réunion Is. in the Indian Ocean. Larvae of *H. madagascariensis* mine the leaves of *Peponidium humbertianum* (Cavaco) (Rubiaceae). Biology and immature stages otherwise remain unknown. Hancock (2005) provided an identification key to Afrotropical species.

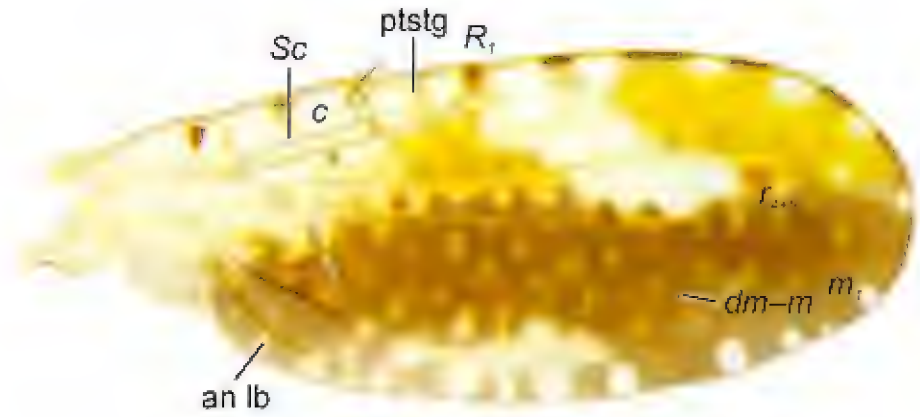
***Hyaloctoides* Munro** (Tephritinae: Pliomelaenini)**.** An endemic genus of four described species: *H. bioculatus* (Bezzi,

1920) from Nigeria; *H. gorgoneus* Hering, 1958 from Cabo Verde; *H. semiater* (Loew, 1861) (Fig. 117) from East and Southern Africa and Yemen; and *H. superhyalinus* from Namibia. Larvae develop in flower heads of *Justicia* and have been found associated with *Monechma* (Acanthaceae). Biology and immature stages otherwise remain unknown. Munro (1963) provided an identification key to species.

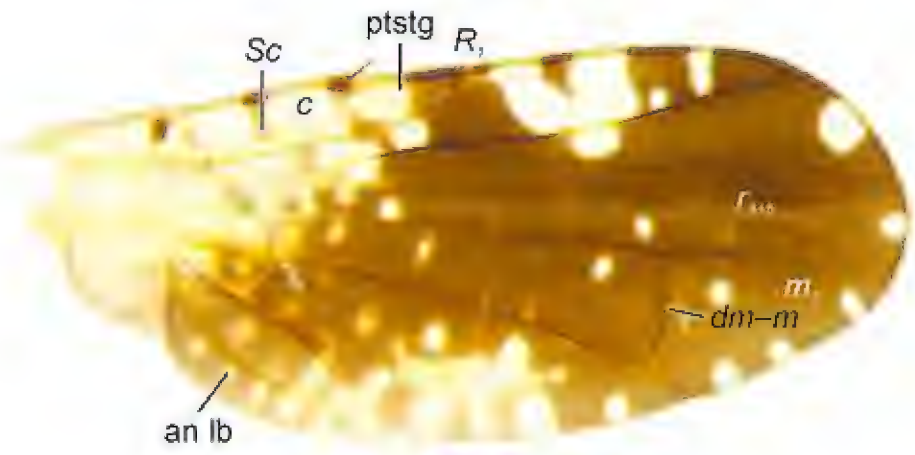
***Hyalotephritis* Freidberg** (Tephritinae: Tephritini)**.** An endemic genus of three described species: *H. australis* (Bezzi, 1924) (Fig. 167), recorded from Namibia and South Africa; *H. complanata* (Munro, 1929), from Kenya, Namibia, Saudi Arabia and South Africa; and *H. planiscutellata* (Becker, 1903), from Egypt to Ethiopia, Saudi Arabia, United Arab Emirates and Yemen. Larvae develop in flower heads of *Geigeria* and *Pluchea* (Asteraceae: Inuleae). Immature stages of *H. planiscutellata* were described by Efflatoun (1925). Freidberg (1979) and Merz & Dawah (2005) enable identification of the species.

***Insizwa* Munro** (Tephritinae: Tephritini)**.** An endemic genus of five described species: *I. dicomala* (Munro, 1935), recorded from Kenya, Namibia and South Africa; *I. goliath* (Bezzi, 1924) and *I. kloofensis* (Munro, 1935) from South Africa; *I. oblita* (Munro, 1929) from Namibia; and *I. striatifrons* Munro, 1929

118 *Leucothryx*



119 *Manicomyia* ♂



120 *Manicomyia* ♂

121 *Platomma*

122 *Pliomelaena*

123 *Pliomelaena*

Figs 71.118–123. Wings of Tephritidae (dorsal views): (118) *Leucothrix oryx* Munro; (119) *Manicomyia chirindana* (Munro) ♂; (120) *Manicomyia stuckenbergi* Freidberg & Han ♂; (121) *Platomma luniferum* (Loew); (122) *Pliomelaena brevifrons* (Bezzi); (123) *P. xyphosiina* Bezzi.

Abbreviations: an lb – anal lobe; *c* – costal cell; *C* – costal vein; *dm* – discal medial cell; *dm–m* – discal medial crossvein; M_1 – first branch of media; m_1 – first medial cell; ptstg – pterostigma; R_1 – anterior branch of radius; r_1 – first radial cell; r_{2+3} – second + third radial cell; R_{2+3} – second branch of radius; r_{4+5} – fourth + fifth radial cells; R_{4+5} – third branch of radius; *Sc* – subcostal vein.

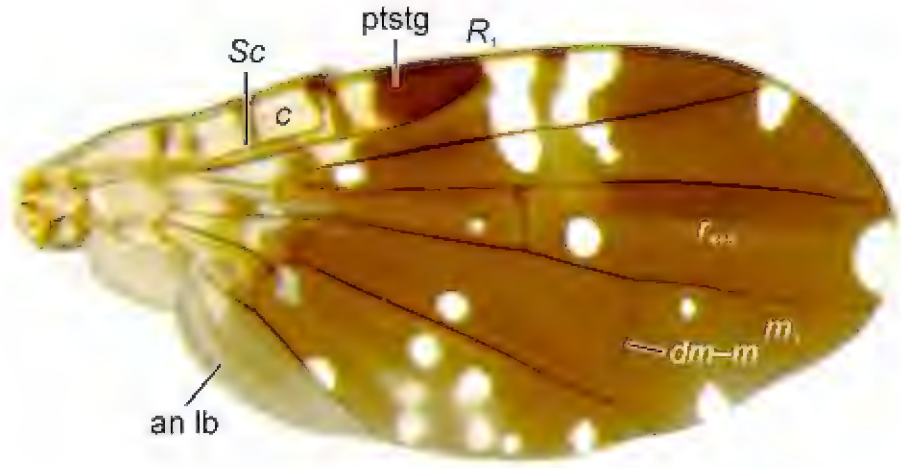
(Fig. 168) from South Africa and Zimbabwe. Larvae develop in flower heads of *Dicoma* and *Gazania* (Asteraceae). Biology and immature stages otherwise remain unknown. No identification key to species is currently available.

***Katonaia* Munro** (Tephritinae: Tephrellini)**.** A genus of three known species, one Palaearctic and two Afrotropical: *K. arushae* Munro, 1935 (Fig. 103), recorded from Ethiopia, Kenya and Tanzania; and an undescribed species from Mt Elgon, Kenya. The Palaearctic *K. aida* Hering, 1938 also occurs in United Arab Emirates in the Afrotropical part of the Arabian Peninsula. Larvae develop in flower heads of *Ballota* and *Leucas* (Lamiaceae). Biology and immature stages otherwise remain unknown. No identification key to species is currently available.

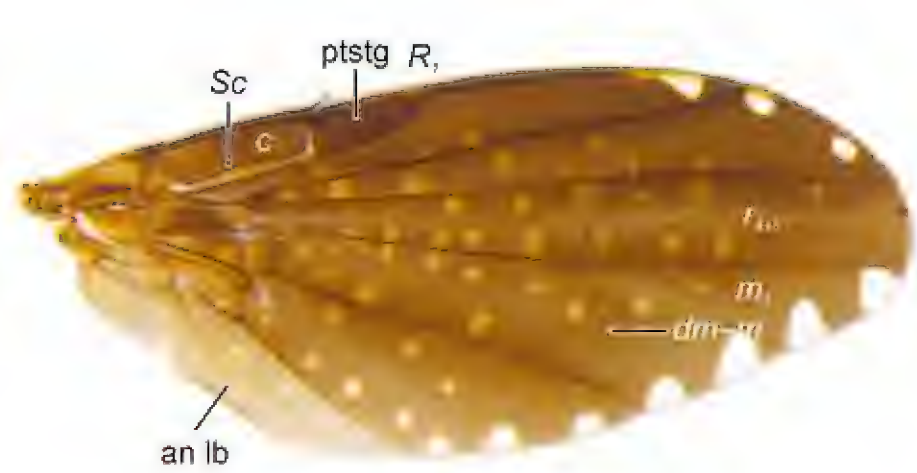
***Labeschatia* Munro** (Phytalmiinae: Acanthonevrini)**.** An endemic monotypic genus with the single described species, *L. circumlineata* Munro, 1967 (Fig. 21), recorded from Malawi and Zambia. Biology and immature stages remain unknown.

***Lethyna* Munro** (Tephritinae: Tephritini)**.** An endemic genus of seven described species (Fig. 137) distributed in north-east, East and Southern Africa, mainly at high elevations. Larvae develop in flower heads of *Helichrysum* (Asteraceae). Biology and immature stages otherwise remain unknown. Munro (1957*a*) provided an identification key to species.

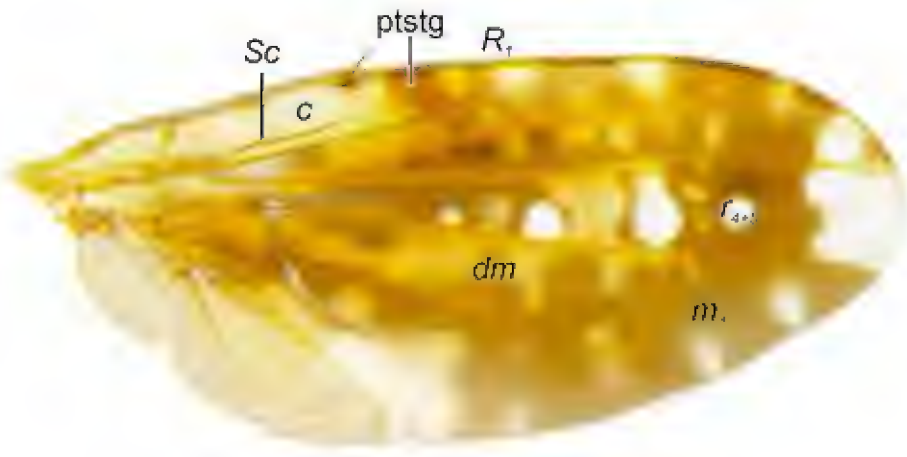
***Leucotaeniella* Bezzi** (Dacinae: Gastrozonini)**.** An endemic genus of four described species (Fig. 67) distributed in the



124 *Pseudafreutreta*

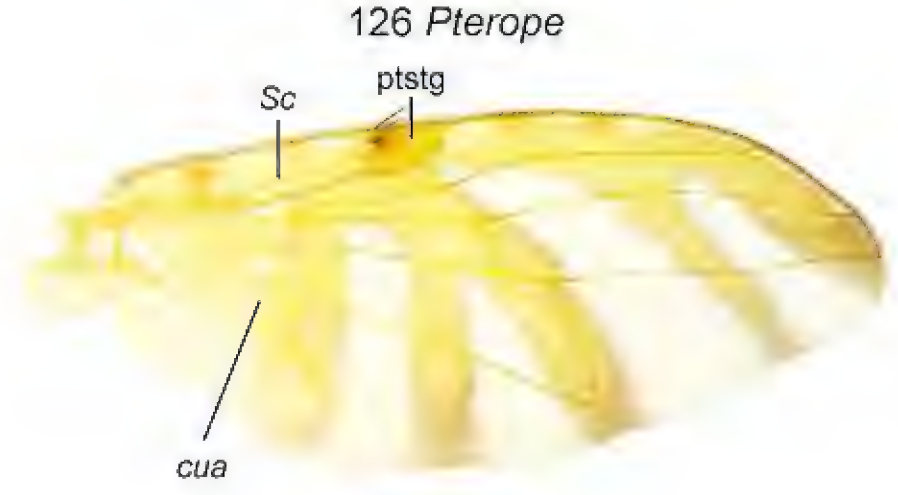


125 *Pseudafreutreta*



126 *Pterope*

127 *Triandomelaena*



128 *Xenodorella*

129 Undescribed genus A ♀

Figs 71.124–129. Wings of Tephritidae (dorsal views): (124) *Pseudafreutreta diaphasis* (Bigot); (125) *Ps. fatua* Hering; (126) *Pterope* sp.; (127) *Triandomelaena albina* (Bezzi); (128) *Xenodorella mira* Munro; (129) Undescribed genus A ♀.

Abbreviations: an lb – anal lobe; *c* – costal cell; C – costal vein; *cua* – anterior cubital cell; *dm* – discal medial cell; *dm–m* – discal medial crossvein; m_1 – first medial cell; ptstg – pterostigma; R_1 – anterior branch of radius; r_{4+5} – fourth + fifth radial cells; *Sc* – subcostal vein.

continental Afrotropics from Sudan to Angola and Zimbabwe. It was referred to the tribe Gastrozonini by Kovac *et al*. (2006) and appears to be most closely related to *Clinotaenia*. Biology and immature stages remain unknown. Hancock (1999) provided an identification key to species.

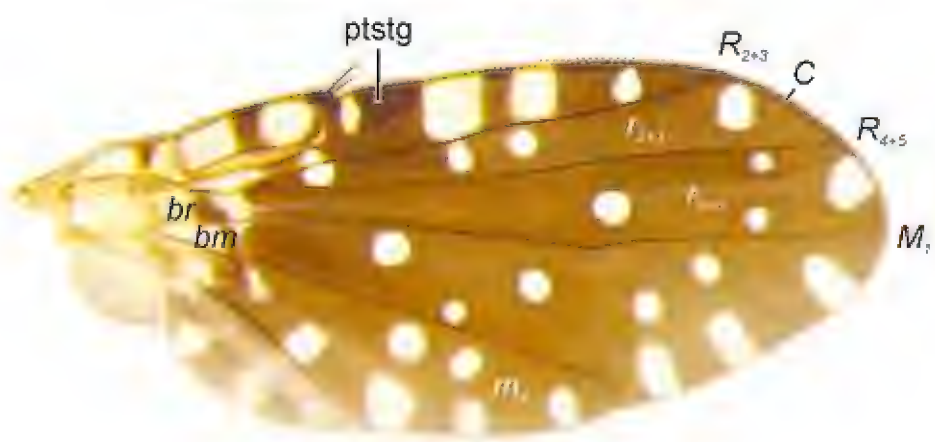
Leucothrix **Munro** (Tephritinae: Pliomelaenini)**.** An endemic genus of three described species: *L. barbata* Munro, 1929 from Namibia; and *L. incana* Munro, 1963 and *L. oryx* Munro, 1956 (Fig. 118) from Namibia and western South Africa; plus an additional undescribed species from western South Africa (Hancock *et al*. 2001). Larvae develop in flower buds of *Monechma* (Acanthaceae). Biology and immature stages otherwise remain unknown. Munro (1963) provided an identification key to described species.

Malagaciura **Hancock** (Tephritinae: Tephrellini)**.** An endemic monotypic genus with the single described species, *M. stuckenbergi* Hancock, 1991, confined to Madagascar. Biology and immature stages remain unknown.

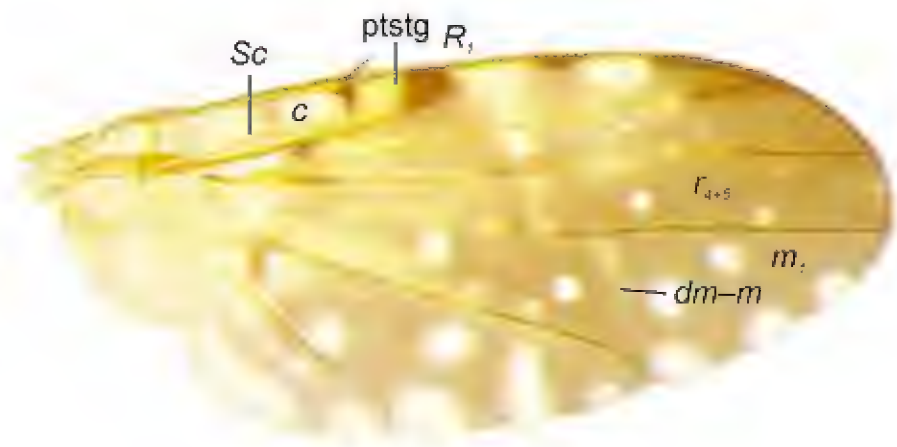
Manicomyia **Hancock** (Tephritinae: Pliomelaenini)**.** An endemic genus of two described species: *M. chirindana* (Munro, 1935) (Fig. 119), recorded from Malawi, Mozambique and Zimbabwe; and *M. stuckenbergi* Freidberg & Han, 2012 (Fig. 120) from Malawi and Zambia. Adults have been swept from

130 Undescribed genus B ♂

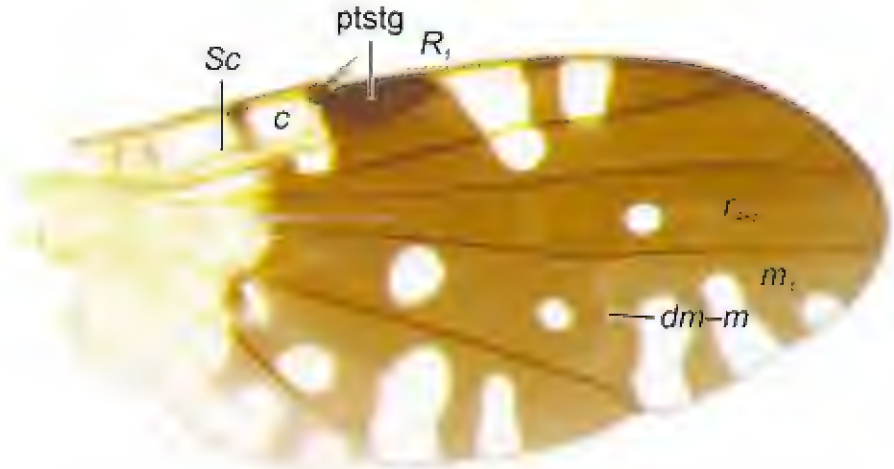
131 *Antoxya*



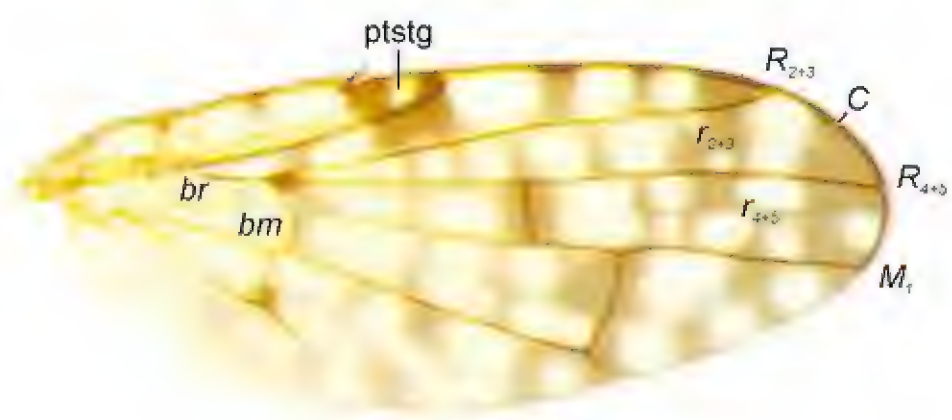
132 *Bezzina*



133 *Chipingomyia* ♂



134 *Chipingomyia* ♀



135 *Campiglossa*

Figs 71.130–135. Wings of Tephritidae (dorsal views): (130) Undescribed genus B ♂; (131) *Antoxya oxynoides* (Bezzi); (132) *Bezzina margaritifera* (Bezzi); (133) *Chipingomyia manica* Hancock ♂; (134) same ♀; (135) *Campiglossa ignobils* (Loew).

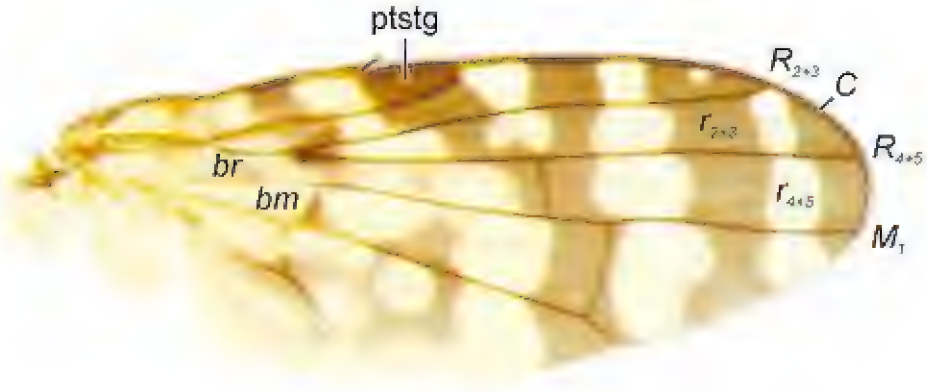
Abbreviations: *bm* – basal medial cell; *br* – basal radial cell; *c* – costal cell; *C* – costal vein; *dm* – discal medial cell; *dm–m* – discal medial crossvein; M_1 – first branch of media; m_1 – first medial cell; m_4 – fourth medial cell; ptstg – pterostigma; R_1 – anterior branch of radius; r_{2+3} – second + third radial cell; R_{2+3} – second branch of radius; r_{4+5} – fourth + fifth radial cells; R_{4+5} – third branch of radius; *Sc* – subcostal vein.

flowers of *Brillantaisia* (Acanthaceae). Biology and immature stages otherwise remain unknown. Freidberg & Han (2012) provided an identification key to species.

Marriottella **Munro** (Tephritinae: Tephritini)**.** An endemic genus of two described species: *M. exquisita* Munro, 1939 (Fig. 147) and *M. sepsoides* Freidberg & Merz, 2006, both from South Africa. Larvae develop in bud galls or flower heads of *Helichrysum* (Asteraceae). Biology and immature stages otherwise remain unknown. Freidberg & Merz (2006) provided an identification key to species.

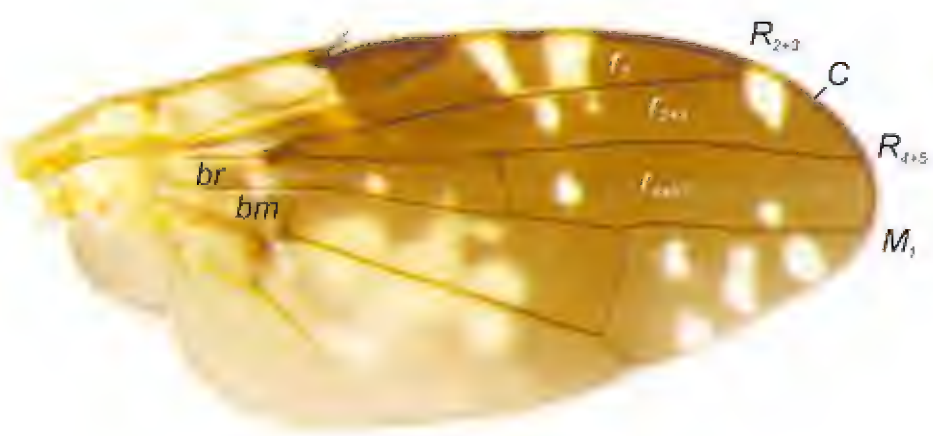
Mastigolina **Munro** (Tephritinae: Tephritini)**.** An endemic genus of two described species: *M. bequaerti* (Munro, 1934) from Liberia and Sierra Leone and *M. rufocomata* Munro, 1947 (Fig. 138) from Kenya; plus an additional undescribed species from Kenya (Copeland *et al*. 2005). This genus appears to be closely related to *Ptosanthus* and was provisionally included in the *Campiglossa*-group by Hancock (2006*a*) and Hancock *et al*. (2001). Biology and immature stages remain unknown. No identification key to species is currently available.

Melanopterella **Freidberg** (Tephritinae: Schistopterini)**.** An endemic genus of four described species: *M. anteroflava* (Munro, 1929), recorded from Namibia and South Africa; *M. nigra* (Bezzi, 1924) (Fig. 88) from Kenya, Liberia, Tanzania and Uganda; *M. spinosa* (Lamb, 1914) from Seychelles and Réunion Is.; and *M. subspinosa* (Bezzi, 1924) from Uganda, plus *ca* 15 additional undescribed species. Copeland *et al*. (2005) used the generic name *"Nigroptera"*, a *nomen nudum*. Larvae develop

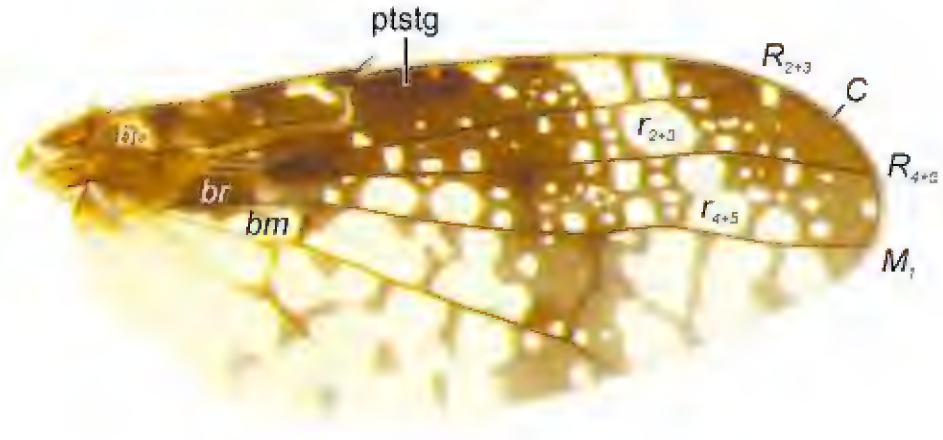


136 *Desmella*

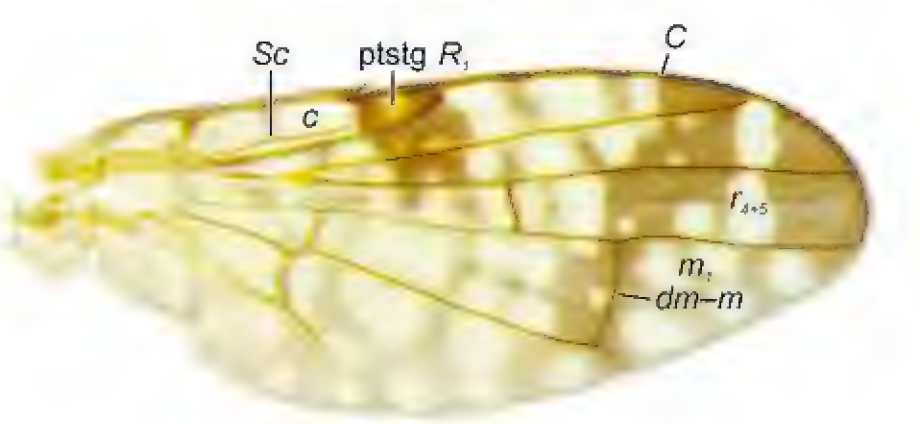
137 *Lethyna*



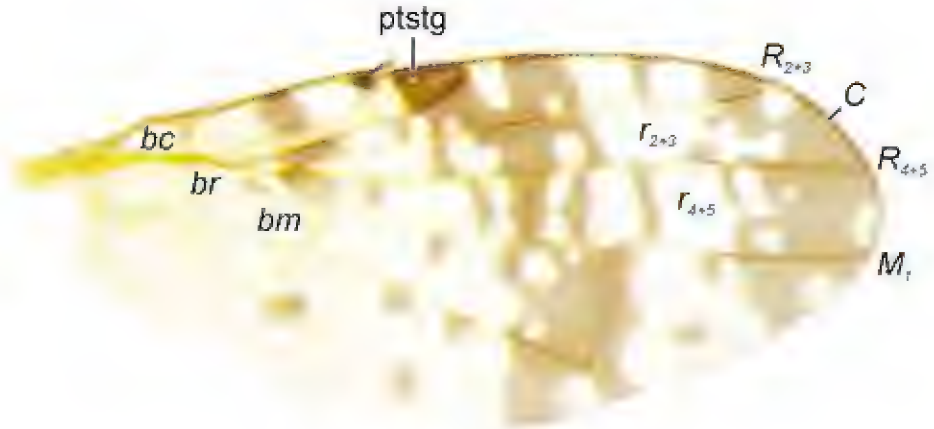
138 *Mastigolina*



139 *Mesoclanis*



140 *Ptosanthus*



141 *Scedella*

Figs 71.136–141. Wings of Tephritidae (dorsal views): (136) *Desmella anceps* (Loew); (137) *Lethyna gladiatrix* (Bezzi); (138) *Mastigolina rufocomata* Munro; (139) *Mesoclanis polana* (Munro); (140) *Ptosanthus helvus* (Loew); (141) *Scedella caffra* (Loew).

Abbreviations: *bc* – basal costal cell; *bm* – basal medial cell; *br* – basal radial cell; *c* – costal cell; *C* – costal vein; *dm–m* – discal medial crossvein; M_1 – first branch of media; m_1 – first medial cell; ptstg – pterostigma; R_1 – anterior branch of radius; r_1 – first radial cell; r_{2+3} – second + third radial cell; R_{2+3} – second branch of radius; r_{4+5} – fourth + fifth radial cells; R_{4+5} – third branch of radius; *Sc* – subcostal vein.

in flower heads of several genera of Asteraceae, including *Aspilia*, *Guizotia*, *Inula* and *Vernonia*. Biology and immature stages otherwise remain unknown. The genus is in need of revision and no identification key to species is currently available.

***Meracanthomyia* Hendel** (Trypetinae: Adramini)**.** A genus of eight known species occurring in the Afrotropical and Oriental Regions. Two species occur in the Afrotropics: *M. antennata* (Hendel, 1912) (Fig. 30), recorded from Ghana, Kenya and possibly Angola; and an undescribed species with metallic colouration from Madagascar. Biology and immature stages remain unknown.

***Mesoclanis* Munro** (Tephritinae: Tephritini)**.** An endemic genus of eight described species (Fig. 139) distributed in Southern Africa, plus a possibly undescribed species from Namibia (Hancock *et al*. 2001). A putative Oriental species was regarded as a mislabelled Australian species of *Austrotephritis* Hancock & Drew by Hancock (2006*b*). Larvae develop in flower heads or stems of *Chrysanthemoides* (Asteraceae) and two species were introduced into Australia for biological control. Biology and immature stages otherwise remain unknown. Munro (1950) provided an identification key to described species.

***Metasphenisca* Hendel** (Tephritinae: Tephrellini)**.** A genus of 25 described species (Fig. 109) occurring in the Afrotropical and Oriental Regions. Of the 23 Afrotropical species, 20 occur in the continental Afrotropics, of which three, plus the Palaearctic *M. negeviana* Freidberg, 1974, also occur in the Arabian Peninsula and two, *M. grandidieri* (Bezzi, 1924) and *M. pallidifemur* Hancock, 1991, are confined to Madagascar. Larvae develop in the seed pods and flower heads of various genera of Acanthaceae. Biology and immature stages otherwise remain unknown. Munro (1947) provided an identification key to, and illustrations of, most Afrotropical species (mostly as *Isoconia*) and Hancock (1991*b*) keyed the two Malagasy species. Two further species, *M. quinquimaculata* (Macquart, 1846) (unrecognisable due to its broken scutellar setae) and *M. transilis* (Munro, 1947), were placed in synonymy with *M. tetrachaeta* (Bezzi, 1918) and *M. parallela* Hering, 1935 by Hancock (2006*a*) and Hancock *et al*. (2003), respectively.

***Microtreta* Freidberg** (Tephritinae: Schistopterini)**.** An endemic genus of five described species (Fig. 89); four distributed in East Africa and one, *M. deemingi* Freidberg, 2002, in Oman, in the Afrotropical part of the Arabian Peninsula. Larvae develop in flower heads of *Vernonia* (Asteraceae). Freidberg (2002) described the larva and puparium and provided an identification key to species.

***Migmella* Munro** (Tephritinae: Tephritini)**.** An endemic genus of four described species: *M. amplifrons* (Bezzi, 1920) and *M. planifrons* (Loew, 1861) (Fig. 148) from South Africa; and *M. elgonensis* Munro, 1957 and *M. scotia* Munro, 1957 from Kenya. Larvae probably develop on Asteraceae: *M. elgonensis* was collected on *Arthemisia afra* Jacq. ex Willd. Biology and immature stages otherwise remain unknown. No identification key to species is currently available, but Munro (1957*a*) reviewed and illustrated the species.

***Multireticula* Merz** (Tephritinae: Tephritini)**.** An endemic monotypic genus, with the single described species, *M. perspicillata* (Bezzi, 1924) (Fig. 169), recorded from Ethiopia, Kenya and South Africa. Larvae develop in terminal galls on *Helichrysum* (Asteraceae: Inuleae). Biology and immature stages otherwise remain unknown.

***Munroella* Bezzi** (Tephritinae: Tephrellini)**.** An endemic monotypic genus, with the single described species, *M. myiopitina* Bezzi, 1924 (Fig. 95), recorded from Kenya, Malawi, South Africa and Zimbabwe. Larvae develop in the flower heads of *Lantana* and *Lippia* (Verbenaceae). Biology and immature stages otherwise remain unknown.

***Munromyia* Bezzi** (Trypetinae: Adramini)**.** An endemic genus of three described species: *M. marsabitensis* Copeland, 2009 from Kenya; *M. nudiseta* Bezzi, 1922 (Fig. 31) from South Africa; and *M. whartoni* Copeland, 2004 from Kenya. Larvae develop in the seeds of wild olives, *Chionanthus* species (Oleaceae). Biology and immature stages otherwise remain unknown. Copeland (2009) provided an identification key to species.

***Myiopardalis* Bezzi** (Trypetinae: Carpomyini)**.** A monotypic genus, with the single described species, *M. pardalina* (Bigot, 1891) (Fig. 35), a largely Palaearctic and western Oriental species, extending into the Afrotropics, possibly as far south as Kenya. Larvae develop in the fruit of Cucurbitaceae. Often regarded as a subgenus or synonym of *Carpomya*. For a partial description of the third-instar larva see White & Elson-Harris (1992: 349).

***Myopites* Blot** (Tephritinae: Myopitini)**.** A primarily Palaearctic genus of 17 described species, including two from the Afrotropics: *M. delottoi* Munro, 1955 (Fig. 71) from Eritrea; and *M. hemixanthus* (Munro, 1931) from Namibia and South Africa; plus at least three additional undescribed Afrotropical species. Larvae develop in flower heads (including galls) of several genera of Asteraceae. Biology and immature stages otherwise remain unknown. Freidberg & Norrbom (1999: 605) reviewed the genus, but did not provide an identification key to species.

***Namwambina* Munro** (Tephritinae: Tephritini)**.** An endemic monotypic genus, with the single described species, *N. festinata* Munro, 1957, known only from Uganda. Biology and immature stages remain unknown.

***Neoceratitis* Hendel** (Dacinae: Ceratitidini)**.** A genus of six described species occurring in the Afrotropical and Palaearctic Regions. Four occur in the Afrotropics: *N. albiseta* De Meyer & Freidberg, 2012 from Madagascar; *N. cyanescens* (Bezzi, 1923) from Comoros, Madagascar, Mauritius and Réunion Is.; *N. efflatouni* (Hendel, 1931) (Fig. 57) from Egypt and Israel to Sudan, Saudi Arabia and United Arab Emirates; and *N. lycii* (Coquillett, 1901) (Fig. 58) from Namibia, South Africa and Tanzania. A fifth species, *N. flavoscutellata* Merz & Dawah, 2005, occurs in Palaearctic Saudi Arabia. Larvae develop in the fruit of Solanaceae, particularly *Lycium*. Biology and immature stages otherwise remain unknown. De Meyer & Freidberg (2012) provided an identification key to species.

***Nippia* Munro** (Dacinae: Ceratitidini)**.** An endemic genus with two described species: *N. alboscutellata* Munro, 1929 from South Africa; and *N. reticulata* Hancock, 1985, recorded from Cameroon and Zambia. Additional undescribed species are known from Kenya (Copeland *et al*. 2005) (Fig. 56) and Nigeria. Males of *N. reticulata* are attracted to methyl eugenol and the genus appears to be related to *Perilampsis*. Biology and immature stages otherwise remain unknown. No identification key to species is currently available.

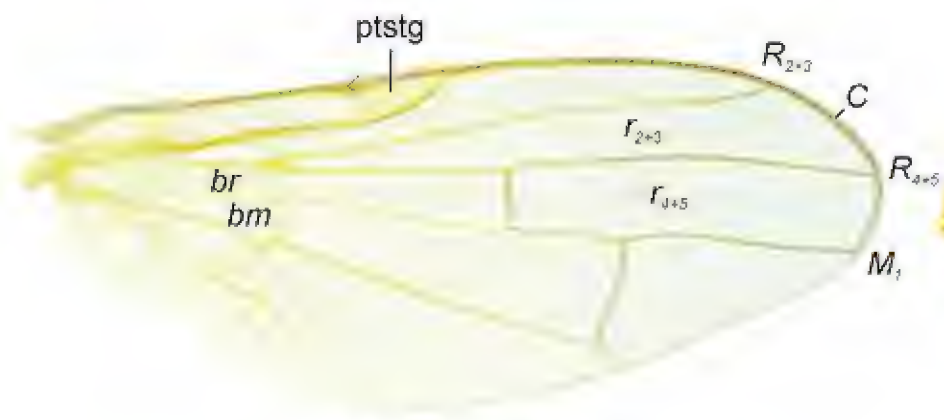
***Notomma* Bezzi** (Trypetinae: Carpomyini)**.** An endemic genus of eight described species (Fig. 36), distributed throughout the continental Afrotropics, as far north as Israel. One species, *N. munroi* Hancock, 1985, is restricted to Madagascar. Larvae form twig galls on *Dicrostachys* and *Vachellia* (Fabaceae). Biology and immature stages otherwise remain unknown. Munro (1952) provided an identification key to seven species, with the eighth differentiated by Hancock (1985*a*).

***Notommima* Freidberg & Copeland** (Trypetinae: Carpomyini)**.** An endemic monotypic genus, with the single described species, *N. parallela* Freidberg & Copeland, 2006 (Fig. 37), known only from Kenya. Larvae develop in the fruit of *Hunteria zeylanica* (Retz.) Gardner ex Thwaites (Apocynaceae). Biology and immature stages were described by Freidberg & Copeland (2006). The genus was considered a close ally of *Notomma* by Freidberg & Copeland (2006).

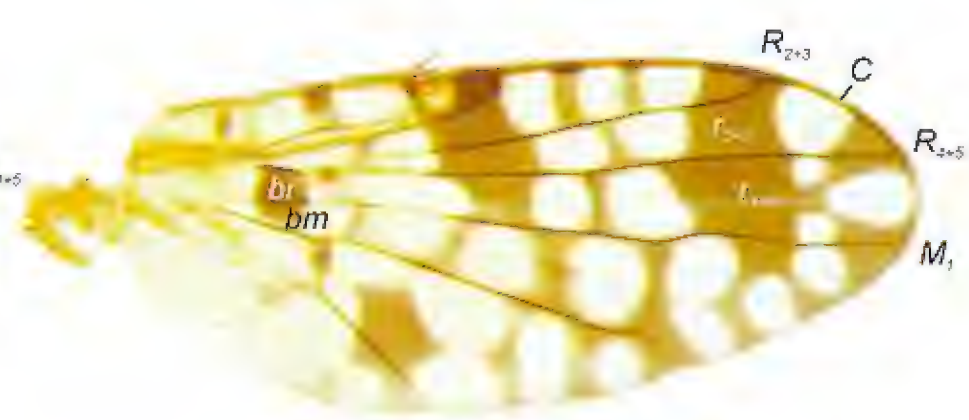
***Notommoides* Hancock** (Trypetinae: Trypetini)**.** An endemic genus of two described species: *N. albida* Freidberg, 1994 (Fig. 44), recorded from Cameroon and Gabon; and *N. pallidiseta* Hancock, 1986 from Mozambique. Biology and immature stages remain unknown. Freidberg (1994) and Hancock (2005) provided identification keys to species.

***Ocnerioxa* Speiser** (Phytalmiinae: Acanthonevrini)**.** An endemic genus of 11 described species (Fig. 22) distributed in East, Southern and West Africa. Larvae develop beneath the bark of *Cussonia* (Araliaceae) trees. Biology and immature stages otherwise remain unknown. Munro (1967) provided an identification key to species.

Ocnerioxyna Séguy (Tephritinae: Tephrellini)**.** An endemic Afrotropical genus of three described species: *O. gracilis* (Loew, 1861), recorded from Malawi and South Africa; *O. hemilea*



142 *Tanaica*



143 *Euaresta*

144 Undescribed genus C

145 *Elgonina*

146 *Gymnosagena*

147 *Marriottella*

Figs 71.142–147. Wings of Tephritidae (dorsal views): (142) *Tanaica hyalipennis* (Bezzi); (143) *Euaresta bullans* (Wiedemann); (144) Undescribed genus C; (145) *Elgonina infuscata* Freidberg & Merz; (146) *Gymnosagena unicornuta* Munro; (147) *Marriottella exquisita* Munro.

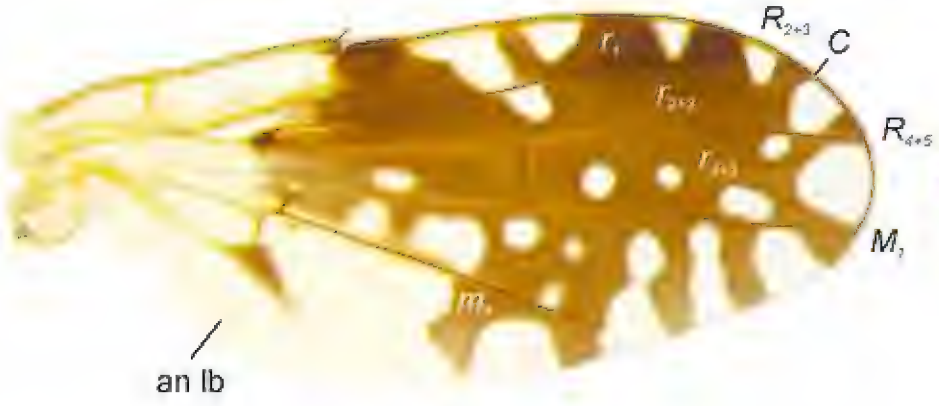
Abbreviations: *bc* – basal costal cell; *bm* – basal medial cell; *br* – basal radial cell; *c* – costal cell; C – costal vein; M_1 – first branch of media; ptstg – pterostigma; r_1 – first radial cell; r_{2+3} – second + third radial cell; R_{2+3} – second branch of radius; r_{4+5} – fourth + fifth radial cells; R_{4+5} – third branch of radius.

Séguy, 1939 from Ethiopia; and *O. maripilosa* (Munro, 1947) (Figs 110, 111) from Kenya and Uganda; plus an additional undescribed species from Yemen (Merz *et al*. 2006). Larvae develop in seed capsules of *Phaulopsis* and *Ruellia* (Acanthaceae). Biology and immature stages otherwise remain unknown. Munro (1947) reviewed the genus (as *Allotrypes*), but no identification key to species was provided.

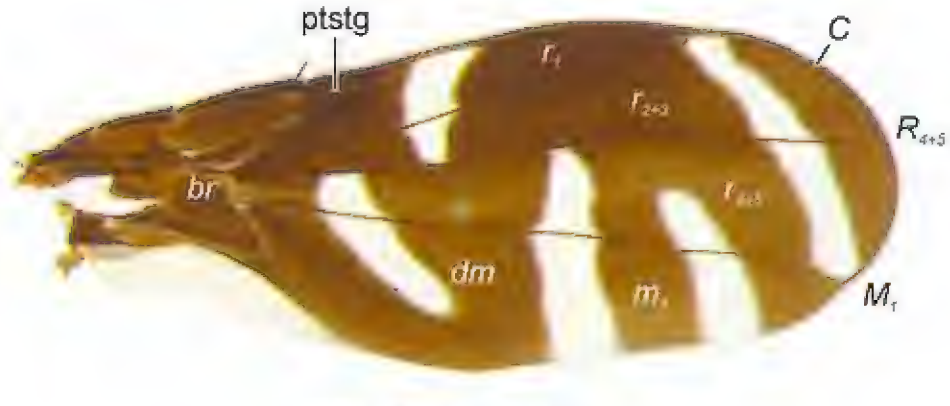
***Ochrobapha* Munro** (Trypetinae: Carpomyini)**.** An endemic monotypic genus, with the single described species, *O. pallescens* Munro, 1938 (Fig. 38), known only from Democratic Republic of Congo. This genus is of uncertain relationships and is provisionally included in the tribe Carpomyini. Biology and immature stages remain unknown.

***Oedaspis* Loew** (Tephritinae: Dithrycini: Platensinina)**.** A widespread genus of 48 described species (Figs 78, 79) occurring in the Afrotropical, Australasian, Oriental and Palaearctic Regions. Sixteen described and one undescribed species are known from the continental Afrotropics, with three species in Madagascar. Adults of all Afrotropical species have greatly reduced mouthparts (Fig. 7) and apparently do not feed. Larvae form stem galls on various genera of Asteraceae. Biology and immature stages otherwise remain unknown. Freidberg & Kaplan (1992) provided an identification key to the 17 Afrotropical species.

***Oedoncus* Speiser** (Tephritinae: Tephrellini)**.** An endemic monotypic genus, with the single described species,



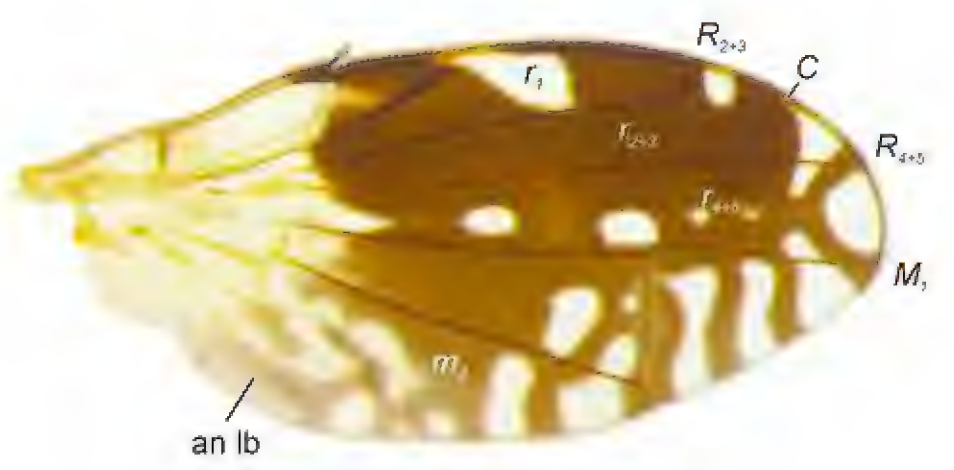
148 *Migmella*



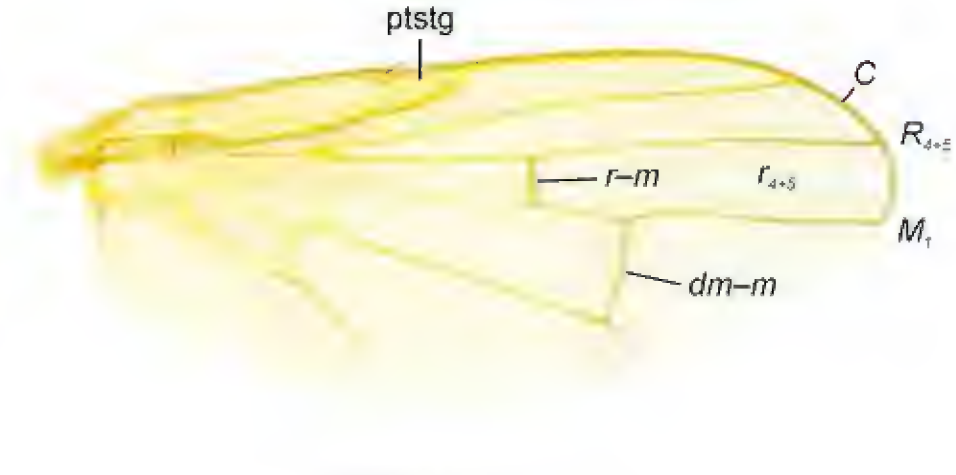
149 *Peratomixis*

150 *Spathulina*

151 *Tephritoresta*



152 *Tephritoresta*



153 *Acronneus*

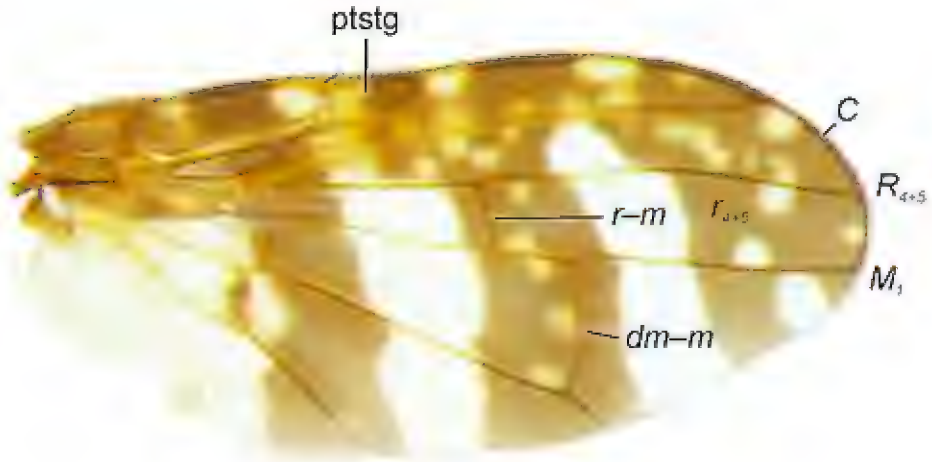
Figs 71.148–153. Wings of Tephritidae (dorsal views): (148) *Migmella planifrons* (Loew); (149) *Peratomixis miranda* Munro; (150) *Spathulina* sp.; (151) *Tephritoresta debilis* Hering; (152) *Tephritoresta* sp.; (153) *Acronneus bryanti* (Munro).

Abbreviations: an lb – anal lobe; *br* – basal radial cell; C – costal vein; *dm* – discal medial cell; *dm–m* – discal medial crossvein; M_1 – first branch of media; m_1 – first medial cell; m_4 – fourth medial cell; ptstg – pterostigma; r_1 – first radial cell; r_{2+3} – second + third radial cell; R_{2+3} – second branch of radius; r_{4+5} – fourth + fifth radial cells; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein.

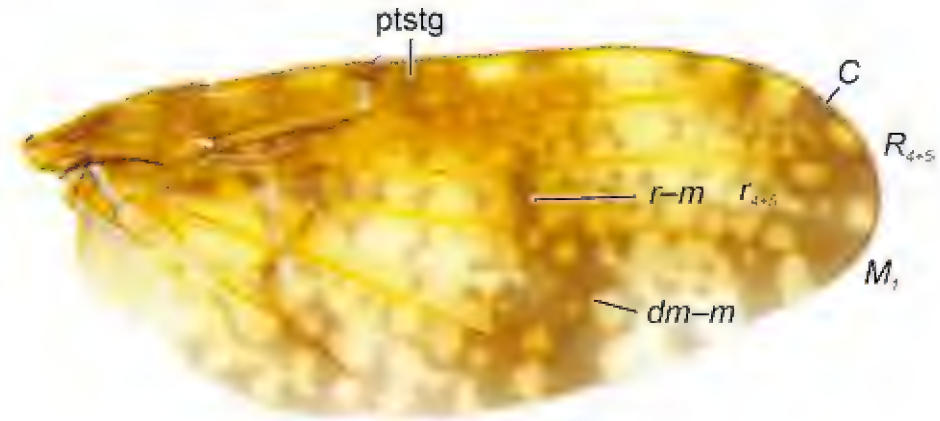
O. taenipalpis Speiser, 1924 (Figs 8, 104), distributed in northeast, East and Southern Africa. This genus appears to be related to *Sphaeniscus* and was transferred to tribe Tephrellini by Hancock *et al*. (2003). Although it most resembles *Sphaeniscus* morphologically, its acanthaceous host-plant suggests better placement in the *Metasphensca* group of genera. The species has been reared in eastern Kenya from a *Barleria*-like species of Acanthaceae (possibly *Ruellia* sp.). Biology and immature stages otherwise remain unknown.

***Oedosphenella* Frey** (incl. *Bevismyia* Munro) (Tephritinae: Tephritini)**.** *Oedosphenella* is an Afrotropical and Palaearctic genus, containing *O. canariensis* (Macquart, 1839) from Canary Is. and *O. auriella* (Munro, 1939) (Fig. 154) from KwaZulu-Natal Province, South Africa. Freidberg & Kaplan (1992) indicated that *Bevismyia* was a probable synonym of *Oedosphenella* and *B. basuto* Munro, 1957 from Lesotho is provisionally included here. Larvae of *O. auriella* develop in spindle-shaped galls on *Senecio* (Asteraceae) (Munro 1939). Biology and immature stages otherwise remain unknown. No identification key to species is currently available.

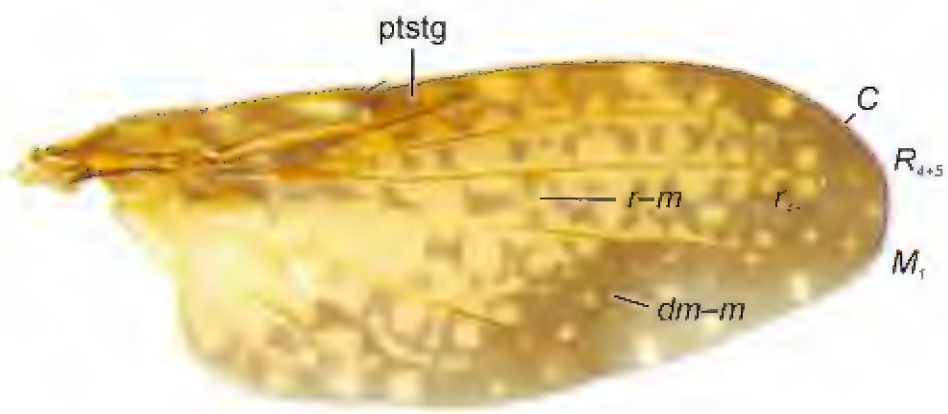
***Orthocanthoides* Freidberg** (Tephritinae: Axiothaumini)**.** An endemic monotypic genus, with the single described species, *O. aristae* Freidberg, 1987, recorded from higher elevations (3,000–3,300 m) in Kenya. Wing pattern and aristal shape (Fig. 11) are sexually dimorphic. This genus appears to be closely related to another high elevation genus, *Axiothauma*. The species is probably associated with giant *Senecio* (Asteraceae). Biology and immature stages otherwise remain unknown.



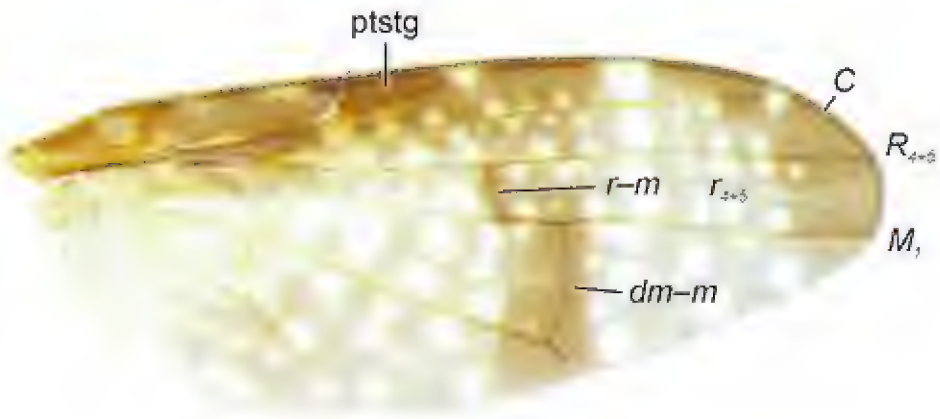
154 *Oedosphenella*



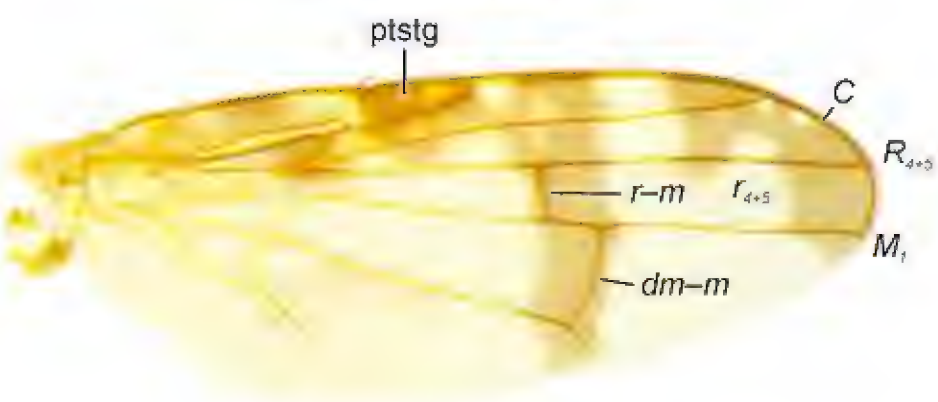
155 *Parafreutreta*



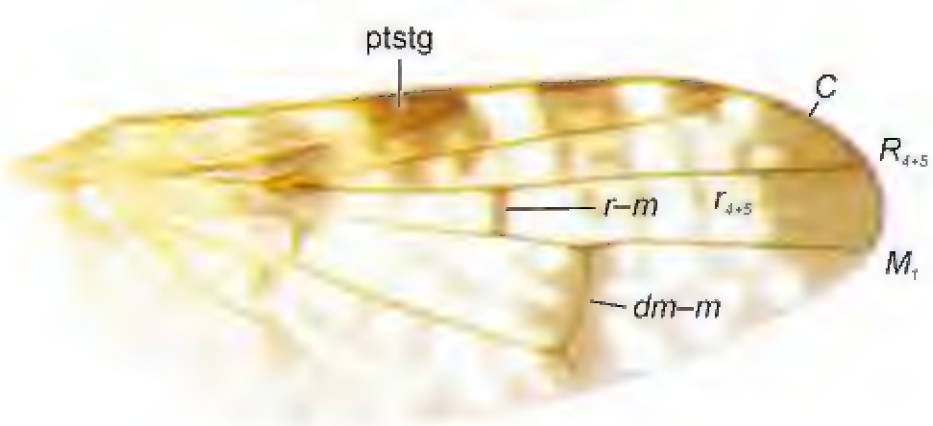
156 *Parafreutreta*



157 *Paratephritis*



158 *Sphenella*



159 *Telaletes*

Figs 71.154–159. Wings of Tephritidae (dorsal views): (154) *Oedosphenella auriella* (Munro); (155) *Parafreutreta producta* Munro; (156) *Parafreutreta* sp.; (157) *Paratephritis incomposita* Munro; (158) *Sphenella marginata* (Fallén); (159) *Telaletes ochracea* (Loew).

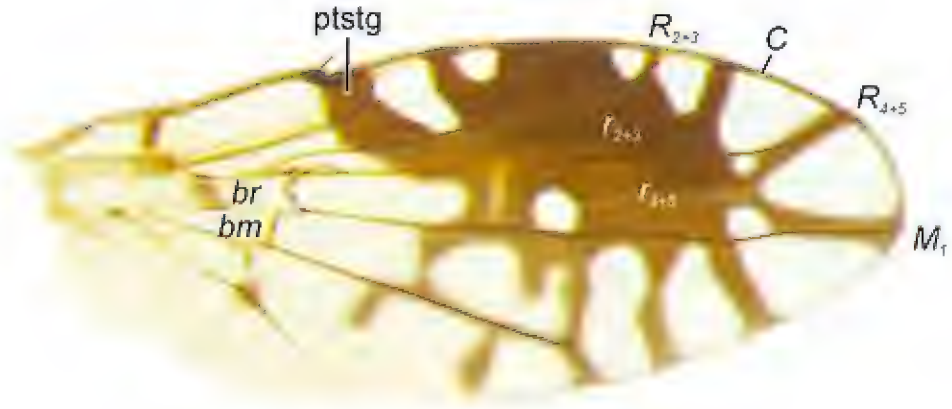
Abbreviations: *C* – costal vein; *dm–m* – discal medial crossvein; M_1 – first branch of media; ptstg – pterostigma; r_{4+5} – fourth + fifth radial cells; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein.

***Oxyaciura* Hendel** (Tephritinae: Tephrellini)**.** A genus of two described species occurring in the Afrotropical and Palaearctic Regions. *Oxyaciura nigra* Merz, 2008, was described from United Arab Emirates and *O. tibialis* (Robineau-Desvoidy, 1830) (Fig. 105), is a largely western Palaearctic species known as far south as Ethiopia, Saudi Arabia and United Arab Emirates in the Arabian Peninsula. Larvae develop in flower heads of *Lavendula* and *Nepeta* (Lamiaceae). Biology and immature stages otherwise remain unknown. Merz (2008) provided an identification key to species, but note that Oriental species were transferred to *Pristaciura* Hendel by Hancock (2010*a*).

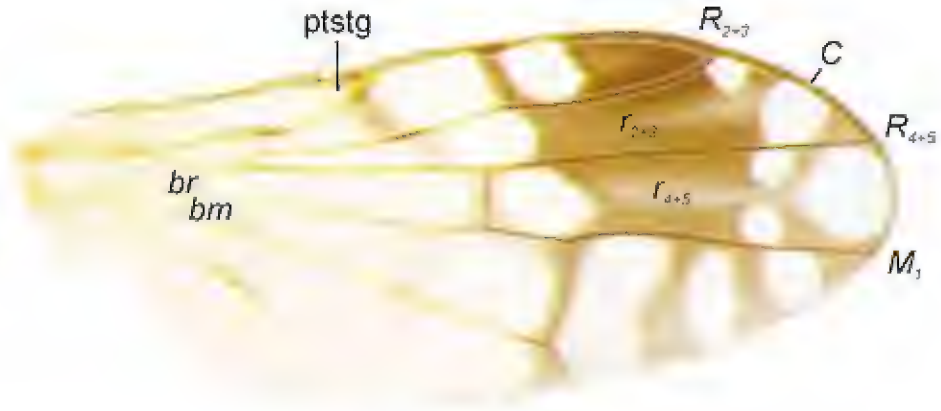
***Paraciura* Hering** (Tephritinae: Tephrellini)**.** An endemic genus with one described species, *P. perpicillaris* (Bezzi, 1920) from West Africa (Fig. 113), but with possibly distinct populations in East Africa (Fig. 114) and Madagascar (Hancock 1991*b*). Biology and immature stages remain unknown.

***Parafreutreta* Munro** (Tephritinae: Tephritini)**.** An endemic genus of 16 described species (Fig. 155), distributed primarily in East and Southern Africa, with one species, *P. mavoana* Munro, 1952, confined to Madagascar. An undescribed species is known from Ethiopia (Fig. 156). Larvae form stem galls on *Crassocephalum* and *Senecio* (Asteraceae). Biology and immature stages otherwise remain unknown. No identification key to species is currently available.

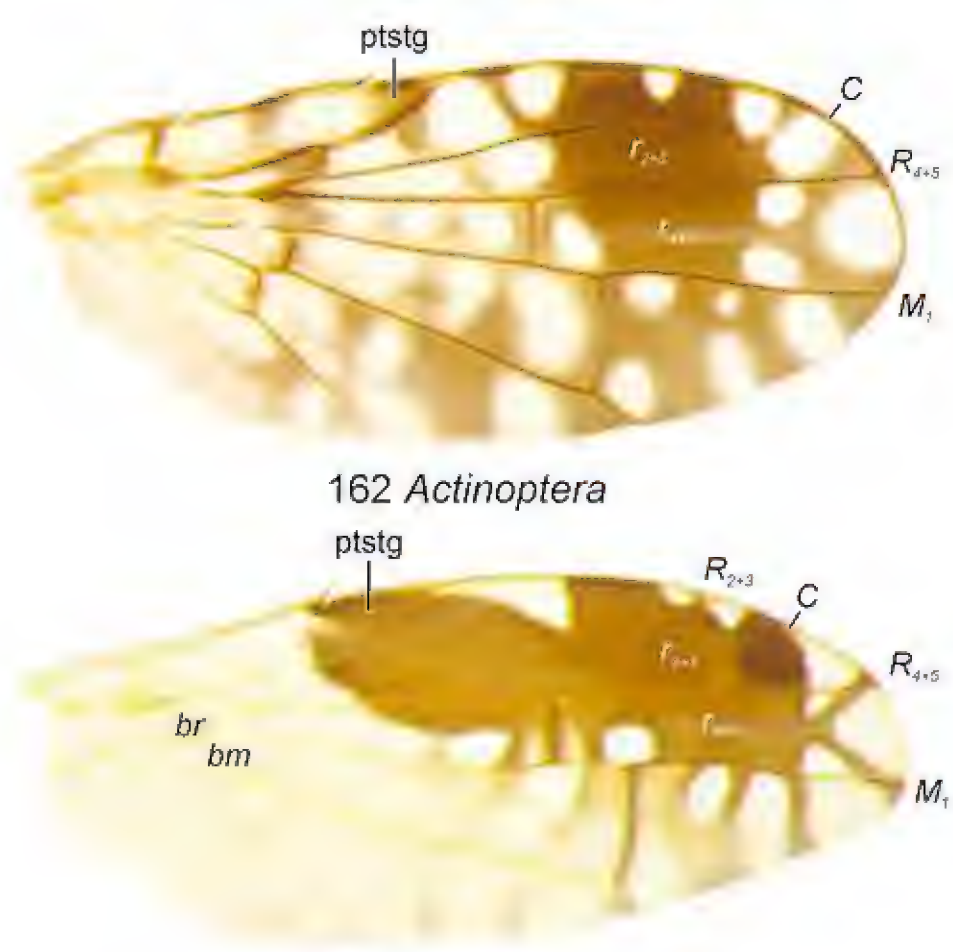
***Parasphenisco ides* Hering** (Tephritinae: Tephrellini)**.** An endemic genus of two described species: *P. binarius* (Loew,



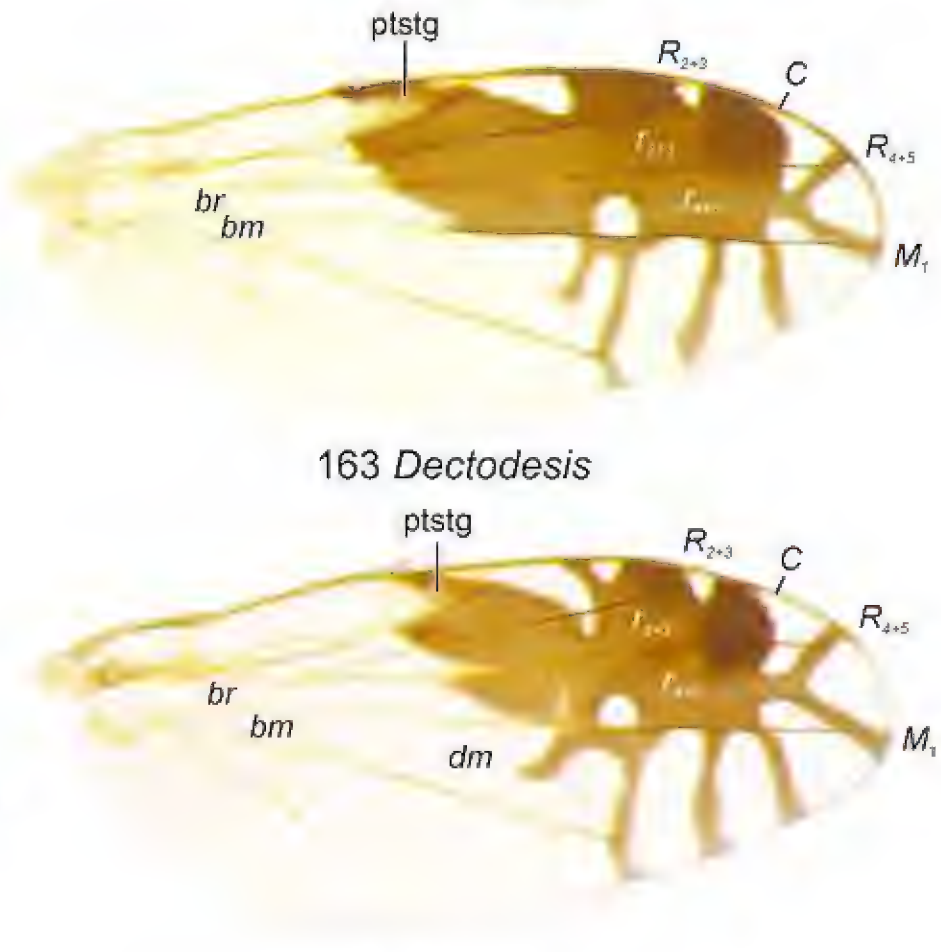
160 *Brachydesis*



161 *Actinoptera*



162 *Actinoptera*



163 *Dectodesis*

164 *Freidbergia*

165 *Goniurellia*

Figs 71.160–165. Wings of Tephritidae (dorsal views): (160) *Brachydesis rivularis* (Bezzi); (161) *Actinoptera peregrina* (Adams); (162) *A. tuckeri* (Bezzi); (163) *Dectodesis confluens* (Wiedemann); (164) *Freidbergia mirabilis* Merz; (165) *Goniurellia munroi* Freidberg.

Abbreviations: *bm* – basal medial cell; *br* – basal radial cell; *C* – costal vein; *dm* – discal medial cell; M_1 – first branch of media; ptstg – pterostigma; r_{2+3} – second + third radial cell; R_{2+3} – second branch of radius; r_{4+5} – fourth + fifth radial cells; R_{4+5} – third branch of radius.

1861) (Fig. 96), from East and Southern Africa, the Indian Ocean islands of Madagascar, Mauritius and Réunion Is., plus Saudi Arabia and Yemen in the Arabian Peninsula; and *P. senarius* (Bezzi, 1924) from Democratic Republic of Congo, Namibia, Uganda and Zambia. Larvae develop in flower heads of *Lantana* and *Lippia* (Verbenaceae). Biology and immature stages otherwise remain unknown. Munro (1947) provided an identification key to species (as *Notoxesis*).

[***Parasphenisc*us Hendel** (Tephritinae: Tephrellini)**.** A monotypic Palaearctic genus, with the single described species, *P. debskii* (Efflatoun, 1924), recorded from Egypt, Israel and Saudi Arabia. The species is not yet recorded from the Afrotropical Region, but might occur. Larvae develop in flower heads of *Stachys* (Lamiaceae). Immature stages were described by Efflatoun (1927).]

***Paratephritis* Shiraki** (Tephritinae: Tephritini)**.** A genus of 11 described species occurring in the Afrotropical, Oriental and Palaearctic Regions. Three species occur in the Afrotropics: *P. incomposita* Munro, 1957 (Fig. 157) from Kenya and Uganda; and *P. karura* Munro, 1957 and *P. umbrifera* Munro, 1957 from Kenya. An additional possibly undescribed species near *P. incomposita* occurs in Zimbabwe (Hancock 1986*b*, 2003*b*). Larvae develop in flower heads of *Senecio* (Asteraceae). Biology and immature stages otherwise remain unknown. Munro (1957*b*) provided an identification key to described Afrotropical species.

***Pediapelta* Munro** (Tephritinae: Tephritini)**.** An endemic monotypic genus, with the single described species, *P. spadicescens* Munro, 1947, known only from South Africa. This genus was restricted by Hancock (2012) (with all other species transferred to *Dicheniotes*) and provisionally assigned to the tribe Tephritini. It is included here, equally provisionally, in the *Campiglossa*-group. Biology and immature stages remain unknown.

***Peratomixis* Munro** (Tephritinae: Tephritini)**.** An endemic monotypic genus, with the single described species, *P. miranda* Munro, 1947 (Fig. 149), known only from Lesotho. This genus is provisionally included in the *Spathulina*-group. Biology and immature stages remain unknown.

***Perilampsis* Bezzi** (Dacinae: Ceratitidini)**.** An endemic genus of 17 described species (Fig. 59) distributed in East, Southern and West Africa. Males of at least two species are attracted to iso- and methyl eugenol. Larvae develop in the seeds of several mistletoe genera (Loranthaceae). Biology and immature stages otherwise remain unknown. De Meyer (2009) provided an identification key to species.

***Perirhithrum* Bezzi** (Tephritinae: Eutretini)**.** A genus of two described species occurring in the Afrotropical and Oriental Regions. The single Afrotropical species, *P. marshalli* Bezzi, 1920 (Fig. 80), is recorded from South Africa and Zimbabwe. The affinities of the genus are uncertain; it was provisionally referred to the Eutretini by Hancock *et al.* (2003), based on morphological similarities with other genera in that tribe, particularly the Nearctic/Neotropical *Paracantha* Coquillett. The Oriental species *P. longiseta* (Hering, 1939) was also referred to the Eutretini by Korneyev (1999*c*: 575) and Hancock (2007*b*). Larvae develop in flowers of *Barleria* (Acanthaceae), a host-plant also utilised by some species of Tephrellini. Biology and immature stages otherwise remain unknown.

***Pherothrinax* Munro** (Tephritinae: Tephritini)**.** A genus of four described species occurring in the Afrotropical and Oriental Regions. Three species are Afrotropical: *P. kohleri* (Hering, 1940) from Cameroon; *P. redimitis* Munro, 1957 (Fig. 170) from Kenya and Uganda; and an undescribed species from Tanzania (Fig. 171). *Pherothrinax woodi* (Bezzi, 1924) (Fig. 172), the type species of *Stelladesis*, was also placed here by Morgulis *et al.* (2015), but not formally transferred. Biology and immature stages remain unknown. No identification key to species is currently available.

***Philophylla* Rondani** (Trypetinae: Trypetini)**.** A genus of 46 described species occurring in the Afrotropical, Australasian, Oriental and Palaearctic Regions. Of the 10 Afrotropical species, five are recorded only from Madagascar and one, *P. seychellensis* (Lamb, 1914), only from Seychelles. Larvae of several Australasian and Oriental species develop in berries of *Clerodendrum* and *Premna* (Verbenaceae). Biology and immature stages otherwise remain unknown. Hancock (2005) provided an identification key to Afrotropical species.

***Platomma* Munro** (Tephritinae: Pliomelaenini)**.** An endemic genus of two described species: *P. luniferum* (Loew, 1861) (Fig. 121) from Namibia, western South Africa and possibly Niger; and *P. nigrantior* Munro, 1963 from Kenya, Namibia, South Africa and Yemen. Larvae develop in flower buds of *Monechma* (Acanthaceae). Biology and immature stages otherwise remain unknown. Munro (1963) provided an identification key to species.

***Pliomelaena* Bezzi** (Tephritinae: Pliomelaenini)**.** A genus of 10 described and several undescribed species, occurring in the Afrotropical, Australasian and Oriental Regions. Five described species occur in East, Southern and West Africa: *P. brevifrons* (Bezzi, 1918) (Fig. 122), *P. discosa* Munro, 1947, *P. exilis* Munro, 1947, *P. stevensoni* Munro, 1937 and *P. xyphosiina* Bezzi, 1924) (Fig. 123), while at least three undescribed species are known from Madagascar. Three other previously included Afrotropical species were transferred to other genera by Hancock *et al.* (2003), while the South African *P. joanetta* Munro, 1947 was synonymised with *Psednometopum nigritum* Munro, 1937 by Hancock (2006*a*). Larvae develop in flower heads of several genera of Acanthaceae. Biology and immature stages otherwise remain unknown. Munro (1947) provided an identification key that included the described Afrotropical species noted above, with *P. aspila* Bezzi, 1924 retained as a synonym of *P. brevifrons* by Hancock (2006*a*).

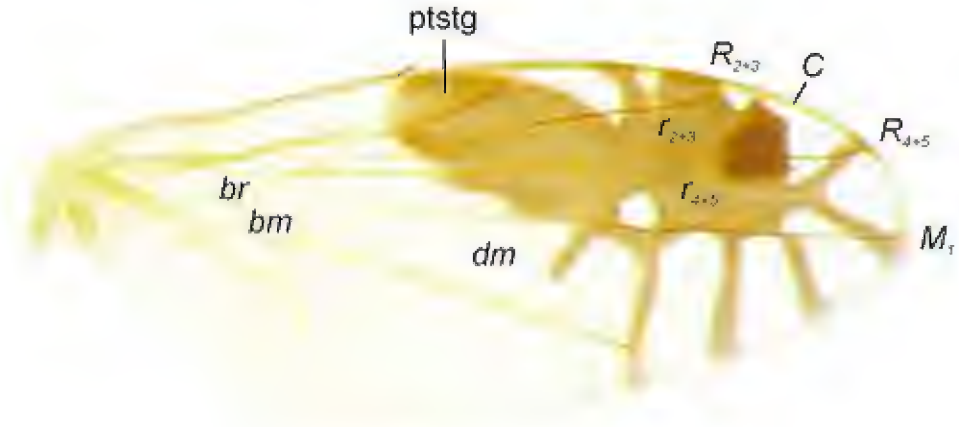
***Procecidochares* Hendel** (Tephritinae: Cecidocharini)**.** A Nearctic and Neotropical genus of 15 described species, with one, *P. utilis* Stone, 1947 (Fig. 76), deliberately introduced into South Africa in 1984 for the biological control of Crofton weed, *Ageratina adenophora* (Sprengel) King & Robinson (Asteraceae) (Freidberg & Mansell 1995). Freidberg & Mansell (1995) also illustrated puparia within a gall.

***Psednometopum* Munro** (Tephritinae: Pliomelaenini)**.** An endemic genus of two described species: *P. aldabrense* (Lamb, 1914) from Seychelles (Aldabra Is.); and *P. nigritum* Munro, 1937 from Ethiopia, Kenya, Namibia, South Africa and Zimbabwe. Specimens from Saudi Arabia and Yemen possibly belong to an undescribed species (Merz & Dawah 2005). Biology and immature stages remain unknown. Hancock (2006*a*) discussed the status of the two described species and noted their differences.

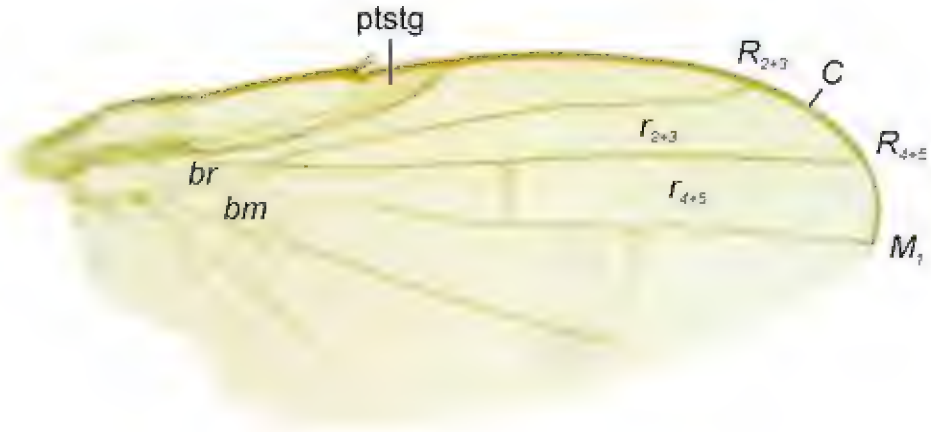
***Pseudafreutreta* Hering** (Tephritinae: Pliomelaenini)**.** A genus of nine described species (Fig. 125) occurring in the Afrotropical and Oriental Regions. Seven described species occur in the Afrotropics, distributed in East, Southern and West Africa, while *P. guttatolimbata* (Enderlein, 1911) and three undescribed species occur in Madagascar. Five Afrotropical species formerly included in the Oriental genus *Platensina* Enderlein were transferred by Hancock *et al.* (2003). Some species, such as *P. guttatolimbata* and *P. katangana* (Munro, 1937), are sexually dimorphic in wing shape and pattern; the female of *P. guttatolimbata* resembles the continental Afrotropical species *P. diaphasis* (Bigot, 1891) (Fig. 124). Larvae develop in flower heads of several genera of Acanthaceae, including *Asystasia* and *Brillantaisia*. Biology and immature stages otherwise remain unknown. Munro (1947) provided an identification key to the five species then known (as *Platensina*), but a key to all species is currently unavailable.

***Pseudomyoleja* Han & Freidberg** (Trypetinae: Trypetini)**.** An endemic genus of three described species: *P. flavicrus* Han & Freidberg, 1994 from Nigeria; *P. nigricrus* Han & Freidberg, 1994 (Fig. 45), from Democratic Republic of Congo and Malawi; and *P. tsaratanana* (Hancock, 1985) from Madagascar. Biology and immature stages remain unknown. Hancock (2005) provided an identification key to species.

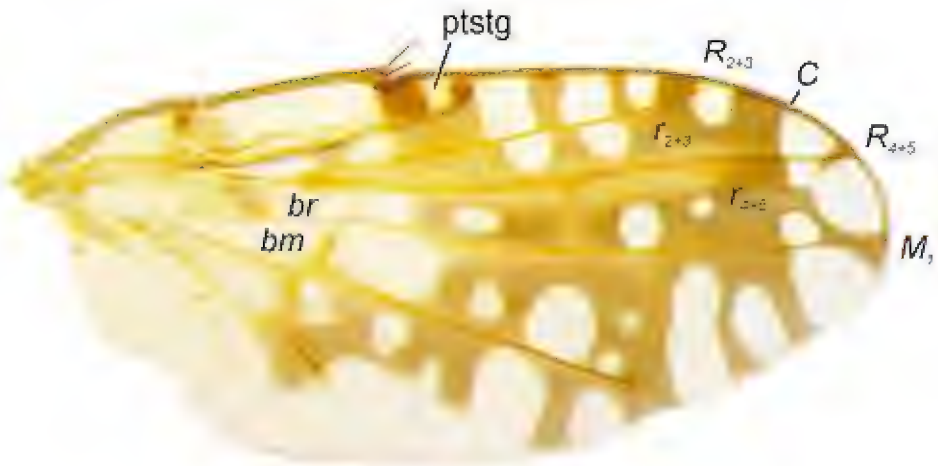
***Pterope* Munro** (Tephritinae: Pliomelaenini)**.** An endemic genus, with the single described species, *P. rubens* Munro, 1957



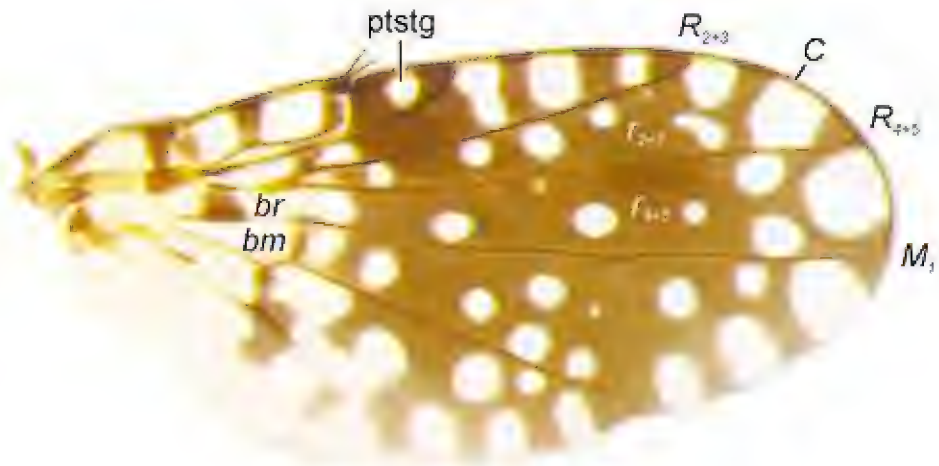
166 *Goniurellia*



167 *Hyalotephritis*



168 *Insizwa*



169 *Multireticula*

170 *Pherothrinax*

171 *Pherothrinax*

Figs 71.166–171. Wings of Tephritidae (dorsal views): (166) *Goniurellia spinifera* Freidberg; (167) *Hyalotephritis australis* (Bezzi); (168) *Insizwa striatifrons* Munro; (169) *Multireticula perspicillata* (Bezzi); (170) *Pherothrinax redimitis* Munro; (171) *Pherothrinax* sp.

Abbreviations: *bm* – basal medial cell; *br* – basal radial cell; C – costal vein; *dm* – discal medial cell; M_1 – first branch of media; ptstg – pterostigma; r_{2+3} – second + third radial cell; R_{2+3} – second branch of radius; r_{4+5} – fourth + fifth radial cells; R_{4+5} – third branch of radius.

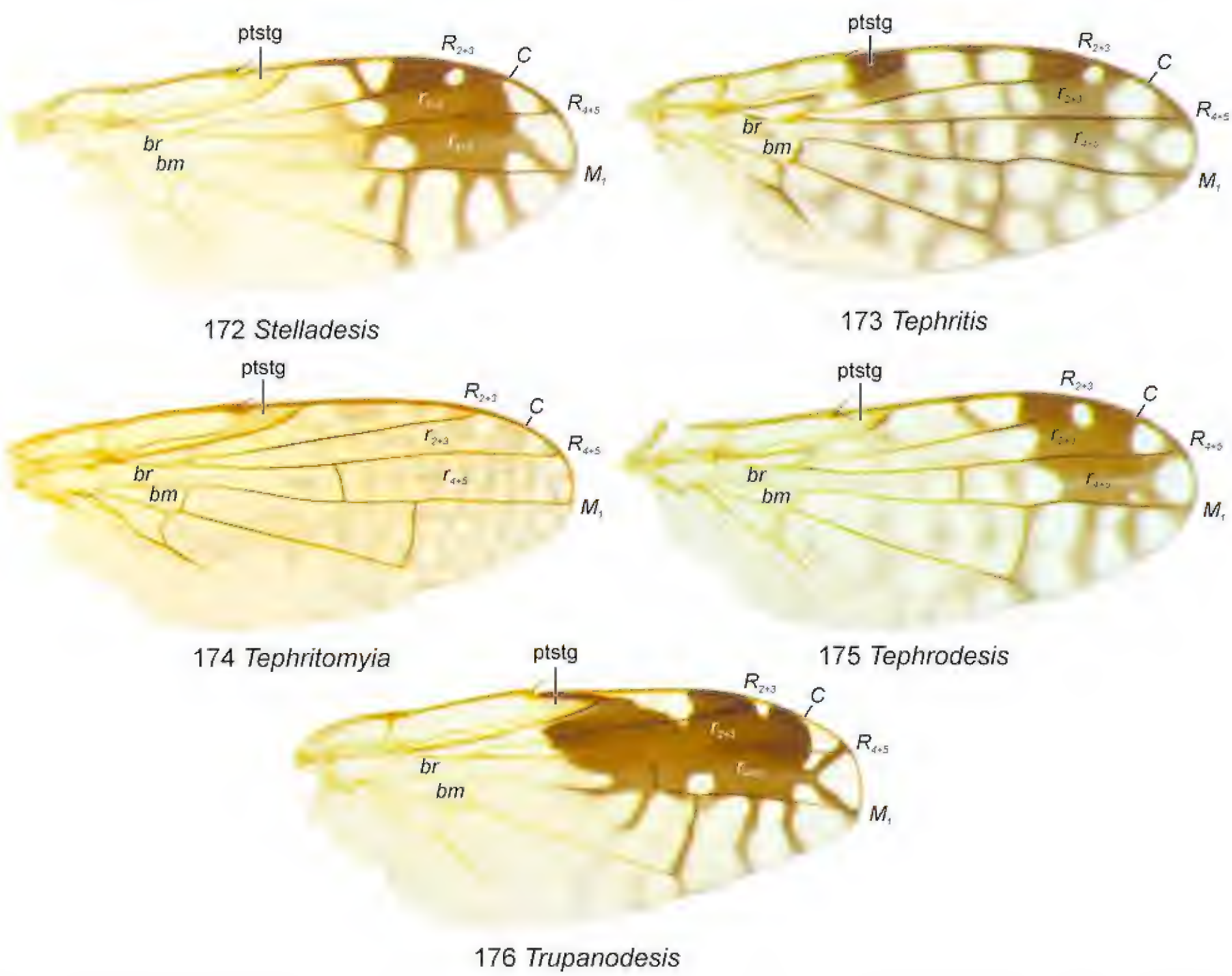
from Uganda, plus an additional undescribed species from Kenya (Fig. 126). It appears to be related to *Manicomyia* and *Pseudafreutreta* (Freidberg & Han 2012; Hancock 2006*a*). Biology and immature stages remain unknown.

Ptiloniola **Hendel** (Phytalmiinae: Acanthonevrini)**.** An endemic genus of three described species: *P. edwardsi* Munro, 1967 from Kenya and Uganda; *P. rotunda* Munro, 1967 from Kenya; and *P. tripunctulata* (Karsch, 1887) (Fig. 23), from East, Southern and West Africa. Biology and immature stages remain unknown. Munro (1967) provided an identification key to species.

Ptosanthus **Munro** (Tephritinae: Tephritini)**.** An endemic genus, with the single described species, *P. helvus* (Loew, 1861) (Fig. 140), recorded from Ethiopia, Kenya, South Africa and Uganda. An additional undescribed species is known from Madagascar. The wing pattern is variable and Munro (1957*a*) regarded several other taxa, including *P. aida* (Hering, 1937) from Ethiopia, as synonyms. Wing vein R_1 has the row of setae adjacent to the subcostal vein (*Sc*) longer than in other tephritine genera. This genus appears to be closely related to *Mastigolina* and was provisionally included in the *Campiglossa*-group by Hancock (2006*a*) and Hancock *et al*. (2001). Biology and immature stages remain unknown.

Pycnella **Munro** (Tephritinae: Tephrellini)**.** An endemic monotypic genus, with the single described species, *P. taomyioides* (Bezzi, 1924), known only from South Africa. This genus is of uncertain relationships and is provisionally included in the *Metasphenisca* group of genera. Biology and immature stages remain unknown.

Rhabdochaeta **de Meijere** (Tephritinae: Schistopterini)**.** A genus of five described and five undescribed species, occurring in the Afrotropical, Australasian and Oriental Regions. The



Figs 71.172–176. Wings of Tephritidae (dorsal views): (172) *Stelladesis woodi* (Bezzi); (173) *Tephritis cinerea* Munro; (174) *Tephritomyia lauta* (Loew); (175) *Tephrodesis pulchella* (Bezzi); (176) *Trupanodesis aurea* (Bezzi).

Abbreviations: *bm* – basal medial cell; *br* – basal radial cell; *C* – costal vein; M_1 – first branch of media; ptstg – pterostigma; r_{2+3} – second + third radial cell; R_{2+3} – second branch of radius; r_{4+5} – fourth + fifth radial cells; R_{4+5} – third branch of radius.

Oriental species *R. mucronata* Hering, 1942 (Fig. 90), described from Sri Lanka, is also recorded from Democratic Republic of Congo, Kenya and Togo in the Afrotropics. This species was previously noted by Freidberg (2002) as possibly *R. pulchella* de Meijere, 1904. Larvae develop in flower heads of *Blumea axillaris* (Lam.) DC. (Asteraceae). Biology and immature stages otherwise remain unknown. The genus is in need of revision and no identification key to species is currently available.

***Rhochmopterum* Speiser** (Tephritinae: Schistopterini)**.** A genus of 14 described (Fig. 91) and numerous undescribed species, occurring in the Afrotropical, Australasian and Oriental Regions. Seven described and *ca* 10 undescribed species occur in the continental Afrotropics and Madagascar, including "*Rhochmopterum* sp. A" *sensu* Hancock (1986*b*, 2003) from Kenya, Madagascar, Tanzania and Zimbabwe, while *R. arcoides* Munro, 1935 is also recorded from Palaearctic Saudi Arabia. Larvae develop in flower heads of several genera of Vernoniae (Asteraceae), primarily *Vernonia*. Biology and immature stages otherwise remain unknown. The genus is in need of revision and no identification key to species is currently available.

***Rivelliomima* Bezzi** (Trypetinae: Rivelliomimini)**.** An endemic monotypic genus, with the single described species, *R. punctiventris* Bezzi, 1924 (Fig. 41), recorded from Mali, South Africa, Zambia and Zimbabwe. Biology and immature stages remain unknown.

***Scedella* Munro** (Tephritinae: Tephritini)**.** A genus of 19 described species (Fig. 141) occurring in the Afrotropical, Australasian and Oriental Regions. Fifteen species occur in the continental Afrotropics, with one species, *S. dissoluta* (Loew, 1861), also recorded from Yemen in the Arabian Peninsula. Two undescribed species are known from Madagascar. Larvae develop in flower heads of Asteraceae. Biology and immature stages otherwise remain unknown. Munro (1957*a*) provided an identification key to described Afrotropical species.

***Schistopterum* Becker** (Tephritinae: Schistopterini)**.** A genus of three described and at least three undescribed species, occurring in the Afrotropical, Australasian, Oriental and Palaearctic Regions. Two described species are Afrotropical: *S. moebiusi* Becker, 1903, distributed over much of the continental Afrotropics, Saudi Arabia, United Arab Emirates, Yemen and the south-western Palaearctic; and *S. longulum* Munro, 1937 from Kenya. Two undescribed species occur in Madagascar while a third, from Namibia (Hancock *et al*. 2003, as *S.* sp. near *longulum*) (Fig. 84), is possibly generically distinct. Larvae develop in flower heads of *Pluchea* or (the Namibian species) *Pechuel-Loeschea leubnitziae* (Kuntze) O.Hoffm. (Asteraceae: Inuleae: Plucheae). *Schistopterum moebiusi* is possibly a complex of species, with at least two corresponding to the two known host-plants of *Pluchea dioscoridis* (L.) DC. and *P. ovalis* (Pers.) DC.; larvae of *S. longulum* develop in *P. sordida* (Vatke) Oliv. & Hiern, those of the two Madagascan species in *P. bojeri* (DC.) Humbert and ?*P. dioscoridis* respectively. Immature stages of *S. moebiusi* were described by Efflatoun (1925). Hardy (1982) provided an identification key to the described species and the three continental Afrotropical species can be separated by characters noted in Hancock *et al*. (2003).

***Schistotephritis* Freidberg** (Tephritinae: Schistopterini)**.** An endemic genus of two described species: *S. acrophthalma* (Bezzi, 1918) (Fig. 92), from Malawi and Zimbabwe; and *S. pacifera* (Munro, 1968) from Ethiopia; plus one undescribed species from Kenya. Larvae develop in flower heads of *Vernonia* (Asteraceae). Biology and immature stages otherwise remain unknown. The genus is in need of revision and no identification key to species is currently available.

***Scleropithus* Munro** (Trypetinae: Carpomyini)**.** An endemic genus, with the single described species, *S. glaphyrochalyps* Munro, 1939 (Fig. 39), known only from South Africa. Larvae develop in the fruit of *Strychnos henningsii* Gilg (Strychnaceae). Biology and immature stages of the species otherwise remain unknown.

***Setoides* Zonstein & Freidberg** (Tephritinae: Schistopterini)**.** An endemic genus of three described species: *S. albolineata* Zonstein & Freidberg, 2006 from Democratic Republic of Congo; *S. mirabilis* Zonstein & Freidberg, 2006 (Fig. 93), from Kenya and Uganda; and *S. usambaraensis* Zonstein & Freidberg, 2006 from Tanzania. Larvae develop in flower heads of *Vernonia* (Asteraceae). Biology and immature stages otherwise remain unknown. Zonstein & Freidberg (2006) provided an identification key to species.

***Soita* Walker** (Trypetinae: Adramini)**.** A genus of six described species, occurring in the Afrotropical, Australasian, Oriental and Palaearctic Regions. A single species occurs in the Afrotropics: *S. ophioneum* (Enderlein, 1920), known only from Equatorial Guinea. The only host record for the genus is as a stem-borer of *Metaplexis japonica* Makino (Apocynaceae: Asclepiadoideae) in Japan. Biology and immature stages otherwise remain unknown. The monotypic genus *Xaniosternum* Enderlein was placed as a synonym of *Soita* by Chen *et al*. (2015), who also provided an identification key to all known species.

***Sosiopsila* Bezzi** (Trypetinae: Callistomyiini)**.** An endemic genus of three allopatric and poorly differentiated species: *S. metadacus* (Speiser, 1915) (Fig. 34), recorded from Cameroon, Ethiopia, Nigeria and possibly Kenya; *S. rotunda* Munro, 1933, described from South Africa; and *S. trisetosa* (Bezzi, 1920), recorded from Malawi, Mozambique, South Africa and Zimbabwe. Adults tend to aggregate on or around plants, resting or flying in short, nervous darting (A. Freidberg, pers. obs.). Biology and immature stages otherwise remain unknown. The relationships of this genus are poorly understood; it was referred to the tribe Callistomyiini by Hancock (2007*c*), who also provided an identification key to species.

***Spathulina* Rondani** (Tephritinae: Tephritini)**.** A largely Afrotropical genus of nine described and at least one undescribed species, eight from the Afrotropics (Ethiopia and Southern Africa), one Palaearctic and one, *S. acroleuca* (Schiner, 1868), widespread across the Afrotropical, Oriental and Australasian Regions, including Madagascar, Saudi Arabia and Yemen in the Arabian Peninsula. Larvae develop in flower heads of Asteraceae: the Palaearctic species *S. sicula* Rondani, 1856 develops in stem galls of *Phagnalon rupestre* (L.) DC. The undescribed Ethiopian species (Fig. 150), closely related to *S. sicula*, was repeatedly observed and collected on *Phagnalon*, although never reared. Biology and immature stages otherwise remain unknown. Munro (1938) provided an identification key to species.

***Sphaeniscus* Becker** (Tephritinae: Tephrellini)**.** A genus of seven described species occurring in the Afrotropical, Australasian, Oriental and Palaearctic Regions. Two species occur in the Afrotropics: *S. filiolus* (Loew, 1869), from Europe south to Ethiopia; and *S. sexmaculatus* (Macquart, 1843), from East and Southern Africa as far north as Sudan, plus the Indian Ocean Islands of Madagascar, Mauritius and Réunion Is., Socotra Is. and Yemen in the Arabian Peninsula. Larvae develop in flower heads of various genera of Lamiaceae. Immature stages of *S. filiolus* were described by Efflatoun (1927). Munro (1947) provided an identification key to species (as *Spheniscomyia*).

***Sphenella* Robineau-Desvoidy** (Tephritinae: Tephritini)**.** A genus of 19 described species occurring in the Afrotropical, Australasian, Oriental and Palaearctic Regions. Eleven species occur in the Afrotropics, all except one, *S. marginata* (Fallén, 1814) (Fig. 158), from the Palaearctic and Saudi Arabia to South Africa, are known only from Southern Africa. An additional undescribed species is known from Madagascar and *S. setosa* Merz & Dawah, 2005, described from Saudi Arabia, might also occur. Larvae develop in flower heads of *Hertia*, *Othonna* and *Senecio* (Asteraceae). Biology and immature stages otherwise remain unknown. Munro (1957*b*) provided an identification key that includes all described Afrotropical species; for *S. setosa* see Merz & Dawah (2005).

***Spinicosta* Freidberg & Norrbom** (Tephritinae: Myopitini)**.** An endemic genus of two described species: *S. agromyzella* (Bezzi, 1924), recorded from Malawi, South Africa and Zimbabwe; and *S. cilipennis* (Bezzi, 1924) (Fig. 72), from Uganda; plus at least six undescribed species (including two from Kenya and one from Cameroon). Larvae develop in flower heads of *Berkheya*, *Ethulia* and *Vernonia* (Asteraceae). Biology and immature stages otherwise remain unknown. Freidberg & Norrbom (1999: 609) reviewed the genus, but no identification key to species is currently available.

***Stamnophora* Munro** (Tephritinae: Myopitini)**.** An endemic genus, with the single described species, *S. vernoniicola* (Bezzi, 1918) (Fig. 73), recorded from East and Southern Africa, plus at least 10 undescribed species, including some from West Africa and Madagascar. Larvae develop in flower heads or stem galls on *Vernonia* (Asteraceae) and gall formation in *S. vernoniicola* was discussed by Munro (1955). Biology and immature stages otherwise remain unknown. Freidberg & Norrbom (1999: 610) reviewed the genus, but no identification key to species is currently available.

***Stelladesis* Merz** (Tephritinae: Tephritini)**.** An endemic genus of five described and at least five undescribed species. Included species were all transferred from *Pherothrinax* by Merz (1999: 648), but *S. woodi* (Bezzi, 1924) (Fig. 172), the type species of *Stelladesis*, was informally returned to it by Morgulis *et al.* (2015). Larvae develop in flower heads of *Vernonia* (Asteraceae: Vernoniae). Biology and immature stages otherwise remain unknown. No identification key to species is currently available.

***Stephanotrypeta* Hendel** (Tephritinae: Pliomelaenini)**.** An endemic genus of three described species: *S. brevicosta* Hendel, 1931, recorded from Kenya and Sudan and Palaearctic Saudi Arabia; *S. taeniaptera* (Bezzi, 1923) from East and Southern Africa; and *S. vittata* Freidberg, 1979 from East Africa, Madagascar and Yemen and Palaearctic Saudi Arabia. *Terpnodesma* Munro is regarded as a synonym (Freidberg 1979; Hancock 2006*a*). *Stephanotrypeta brevicosta* was reared from a flower of *Justicia elliottii* S.Moore (Acanthaceae) in western Kenya. Biology and immature stages otherwise remain unknown. The genus was reviewed and provisionally referred to the *Campiglossa*-group, in the tribe Tephritini by Hancock (2006*a*), who also transferred "*S.*" *nigrofemorata* (Munro, 1929) to *Triandomelaena*, but *Stephanotrypeta* is referred here to the tribe Pliomelaenini, based on its acanthaceous host-plant. Freidberg (1979) provided an identification key to species.

***Tachiniscidia* Malloch** (Tachiniscinae: Tachiniscini)**.** An endemic monotypic genus, with the single described species, *T. africana* Malloch, 1931, recorded from Democratic Republic of Congo and Zimbabwe. Biology and immature stages remain unknown. Korneyev & Norrbom (2006) provided a detailed re-description of the species.

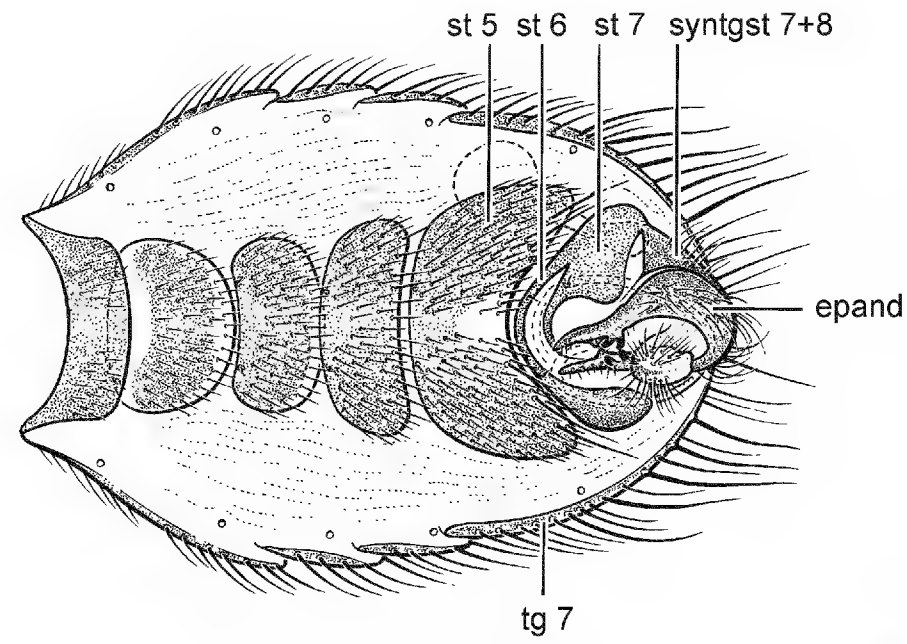
***Tanaica* Munro** (Tephritinae: Tephritini)**.** An endemic genus of three described species: *T. hyalipennis* (Bezzi, 1924) (Fig. 142), recorded from Namibia and South Africa; *T. maculata* Merz & Dawah, 2005 from Ethiopia and Kenya and Palearctic Saudi Arabia; and *T. pollinosa* Merz & Dawah, 2005 from South Africa and Saudi Arabia. Larvae develop in seeds of *Chrysanthemoides* and *Tripteris* (Asteraceae). Biology and immature stages otherwise remain unknown. Merz & Dawah (2005) provided an identification key to species.

***Tanzanimyia* Freidberg, Zonstein & Friedman** (Tephritinae: Schistopterini)**.** An endemic genus of four described species, recorded from Burundi, Kenya, Malawi, Tanzania and Uganda. Larvae develop in flower heads of *Bothriocline* and *Gutenbergia* (Asteraceae: Vernoniae). Biology and immature stages otherwise remain unknown. An identification key to the four species was provided by Freidberg *et al.* (2020).

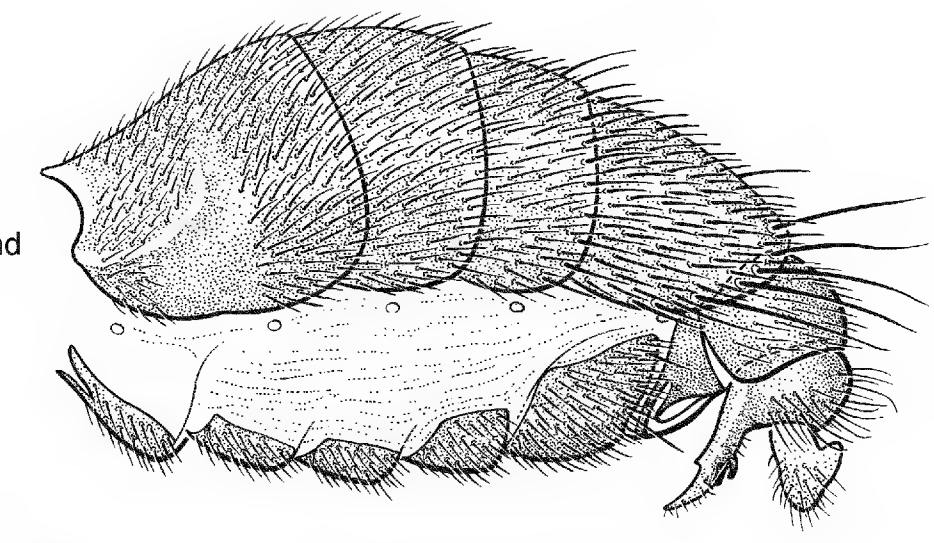
***Taomyia* Bezzi** (Trypetinae: Carpomyini)**.** An endemic genus of four described species: *T. marshalli* Bezzi, 1920 (Fig. 40), recorded from Kenya, South Africa, Tanzania, Uganda and Zimbabwe; *T. mauritiana* Hancock, 1991 from Mauritius; *T. ocellata* (Lamb, 1914) from Seychelles; and *T. pictipennis* Hancock, 1985 from Madagascar. Larvae develop in the fruits of *Dracaena* and *Sansevieria* (Agavaceae). Biology and immature stages otherwise remain unknown. Hancock (1991*a*) provided an identification key to species.

***Tarchonanthea* Freidberg & Kaplan** (Tephritinae: Eutretini)**.** An endemic genus of two described species: *T. coleoptrata* Freidberg & Kaplan, 1993 (Fig. 15), recorded from Kenya and Tanzania; and *T. frauenfeldi* (Schiner, 1868) (Fig. 81), from Namibia and South Africa. Larvae develop in twig galls on *Tarchonanthus* (Asteraceae). Biology and immature stages otherwise remain unknown. Freidberg & Kaplan (1993) provided an identification key to species.

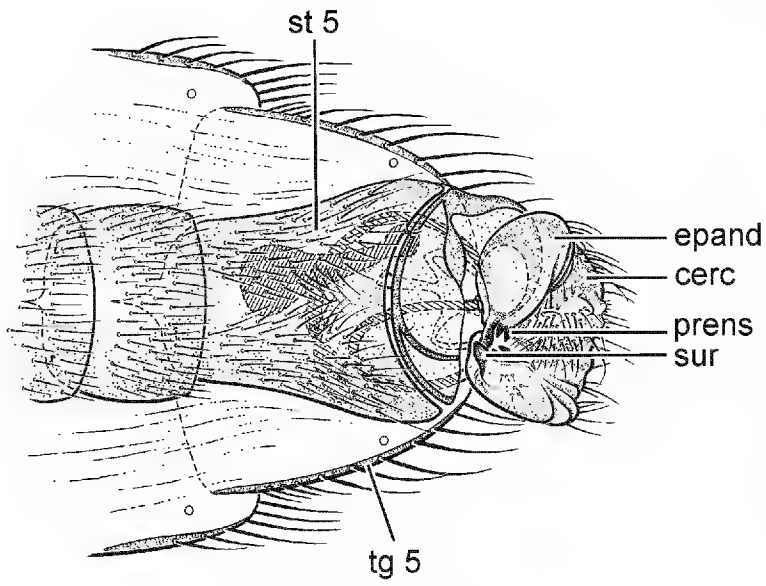
***Telaletes* Munro** (Tephritinae: Tephritini)**.** An endemic genus of two described species: *T. obscuratus* Munro, 1957, recorded from Kenya and Uganda; and *T. ochraceus* (Loew, 1861) (Fig. 159), from Kenya, Lesotho, South Africa and Zimbabwe and Palearctic Saudi Arabia. The genus is placed in the *Sphenella*-group. Larvae develop in flower heads of *Senecio* (Asteraceae). Biology and immature stages otherwise remain unknown. Munro (1957*a*) provided an identification key to species.



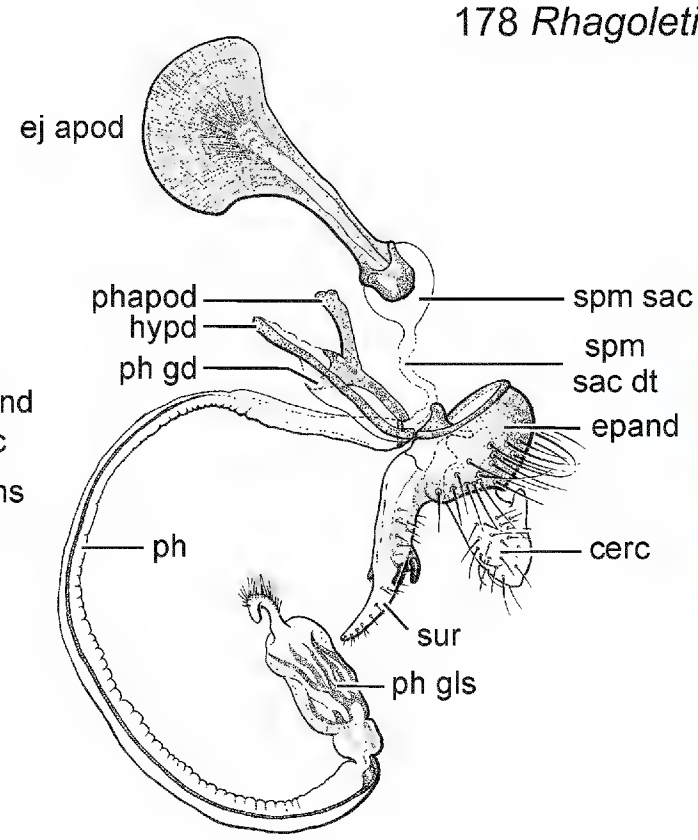
177 *Rhagoletis* ♂



178 *Rhagoletis* ♂

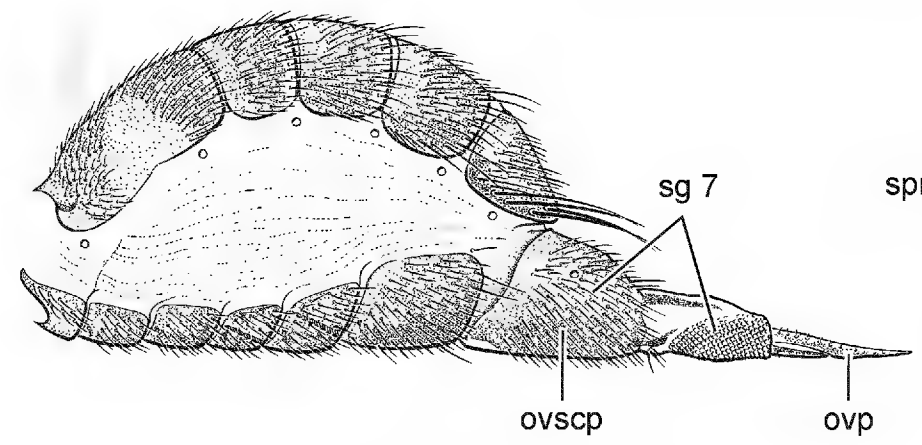


179 *Euaresta* ♂

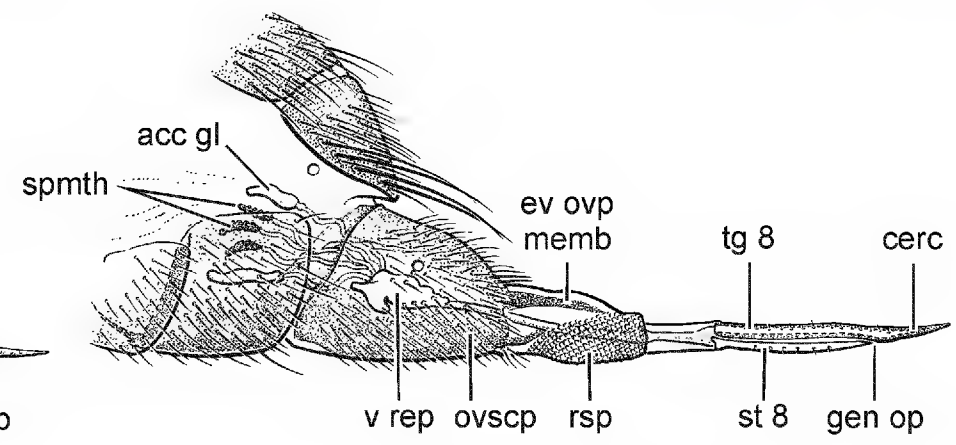


180 *Rhagoletis* ♂

183 *Ceratitoides* ♀



181 *Rhagoletis* ♀

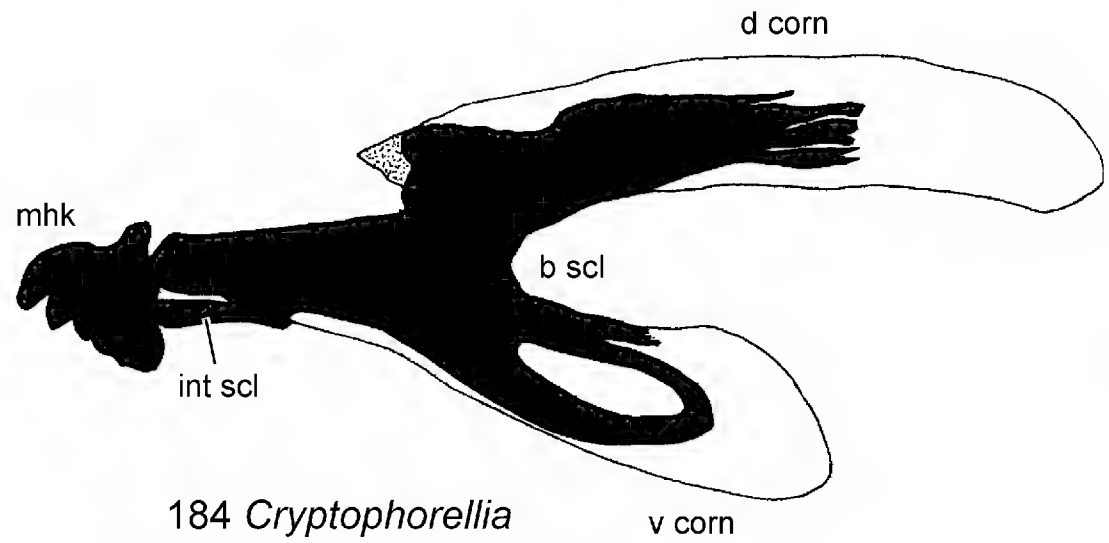


182 *Rhagoletis* ♀

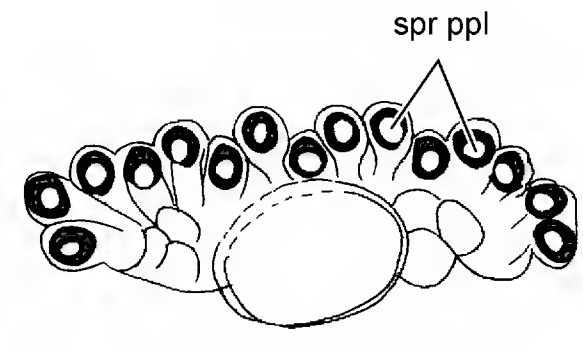
Figs 71.177–183. Abdomens and male and female terminalia of Tephritidae: (177) male abdomen of *Rhagoletis pomonella* (Walsh), ventral view (non-Afrotropical); (178) same, lateral view; (179) male terminalia of *Euaresta aequalis* (Loew), ventral view (non-Afrotropical); (180) detail of male terminalia of *R. pomonella*, lateral view; (181) same, female abdomen, lateral view; (182) same, female terminalia; (183) female aculeus of *Ceratitoides nigromaculatus* Hendel, dorsal view. Figs 177–182 (Foote & Steyskal 1987, figs 38–43).

Abbreviations: acc gl – accessory gland; cerc – cercus; ej apod – ejaculatory apodeme; epand – epandrium; ev ovp memb – eversible ovipositor membrane; gen op – genital opening; hypd – hypandrium; ovp – ovipositor; ovscp – oviscape; ph – phallus; ph gd – phallic guide; ph gls – phallus glans; phapod – phallapodeme; prens – prensisetae; rsp – rasper; sg – segment; spm sac – sperm sac; spm sac dt – sperm sac duct; spmth – spermathecae; st – sternite; sur – surstylus; syntgst – syntergosternite; tg – tergite; v rep – ventral receptacle.

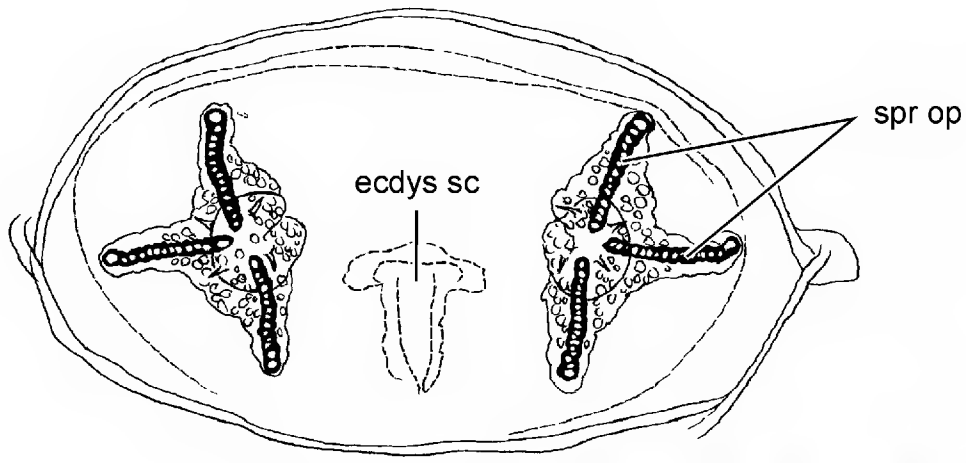
***Tephraciura* Hering** (Tephritinae: Tephrellini)**.** A genus of nine described species, two Oriental and seven Afrotropical, including *T. flavimacula* Hancock, 1991, *T. tulearensis* Hancock, 1991 and a further, undescribed species from Madagascar. Other species occur in East and Southern Africa, with two also recorded from Yemen and one from Socotra Is. (Yemen). Larvae develop in flower heads of various genera of Acanthaceae. Biology and immature stages otherwise remain unknown. Munro (1947) provided an identification key to the Afrotropical species then known (as *Jacotella*) and Hancock (1991*b*) keyed Malagasy species. One previously recognised species, *T. phantasma* Hering, 1935 from Namibia, was placed as a synonym of the widespread *T. oborinia* (Walker, 1849) (Fig. 112) by Hancock *et al*. (2001, 2003).



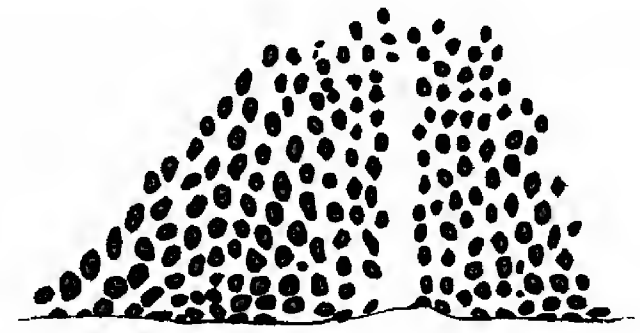
184 *Cryptophorellia*



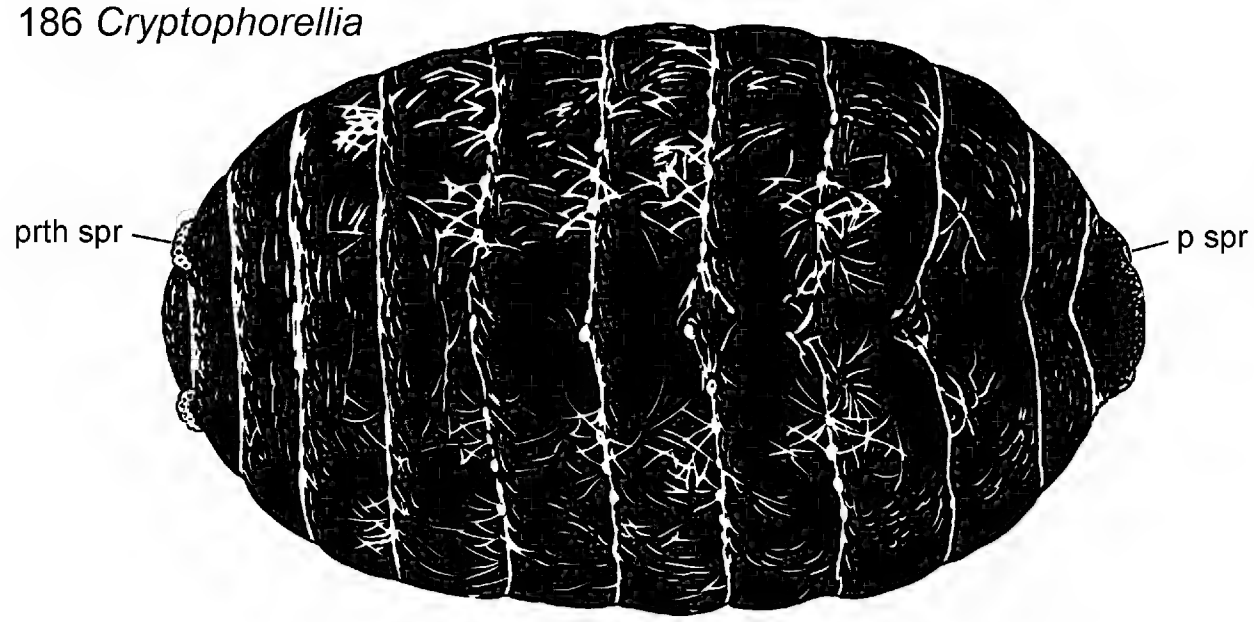
185 *Cryptophorellia*



186 *Cryptophorellia*



187 *Cryptophorellia*



188 *Cryptophorellia*

Figs 71.184–188. Immature stages of Tephritidae: (184) third-instar larval cephaloskeleton of *Cryptophorellia flava* Freidberg & Hancock, lateral view; (185) same, prothoracic spiracle, dorsal view; (186) same, posterior spiracular plate, caudal view; (187) same, detail of creeping welt, lateral view; (188) puparial habitus of *C. peringueyi* (Bezzi), dorsal view. Figs 184–188 (Freidberg & Hancock 1989, figs 59A–D, 60).

Abbreviations: b scl – basal sclerite; d corn – dorsal cornu; ecdys sc – ecdysial scar; int scl – intermediate sclerite; mhk – mouthhook; p spr – posterior spiracle; prth spr – prothoracic spiracle; spr op – spiracular openings; spr ppl – spiracular papillae; v corn – ventral cornu.

***Tephritis* Latreille** (Tephritinae: Tephritini)**.** A genus of *ca* 170 described species occurring in the Afrotropical, Nearctic, Oriental and Palaearctic Regions, with one possibly introduced species in Australia. In addition, there are numerous undescribed species. Two species occur in the Afrotropics: *T. cinerea* Munro, 1931 (Fig. 173), recorded from Lesotho, Malawi and South Africa; and *T. hemimelaena* (Bezzi, 1920) from Ghana, although their generic placement requires further confirmation. Larvae develop in flower heads or stem galls on Asteraceae. Biology and immature stages otherwise remain unknown. The genus is in need of revision and no identification key to species is currently available.

***Tephritomyia* Hendel** (Tephritinae: Tephritini)**.** A genus of 21 described species occurring in the Afrotropical, Oriental and Palaearctic Regions. An additional species, *T. xiphias* (Bezzi, 1924), is regarded as a *nomen dubium*. The 18 Afrotropical species are distributed primarily in Ethiopia, with a few others occurring as far west as Nigeria and as far south as Tanzania. The largely Palaearctic species *T. despoliata* (Hering, 1956), also recorded from Saudi Arabia, and *T. lauta* (Loew, 1861) (Fig. 174), known as far south as Egypt and Iran, might also occur in the region. Larvae develop in flower heads of *Echinops* (Asteraceae: Cardueae). Morgulis *et al*. (2016) provided descriptions of the larva and puparium and an identification key to species.

***Tephritoresta* Hering** (Tephritinae: Tephritini)**.** An endemic genus, with the single described species, *T. debilis* Hering, 1942 (Fig. 151), from Cameroon and Togo. An additional undescribed species (Fig. 152) is known from Madagascar. Biology and immature stages remain unknown.

***Tephrodesis* Merz** (Tephritinae: Tephritini)**.** An endemic Afrotropical genus of three described species: *T. mutila* (Bezzi, 1924), recorded from Ethiopia and South Africa; *T. pulchella* (Bezzi, 1924) (Fig. 175) from Kenya, Namibia and South Africa; and *T. subcompleta* (Bezzi, 1920) from Kenya; plus an undescribed species from Kenya (Merz 1999: 649). Adults have been collected in large numbers on *Tarchonanthea* (Asteraceae: Inuleae), a possible host-plant. Biology and immature stages otherwise remain unknown. The genus is in need of revision and no identification key to species is currently available.

***Themarictera* Hendel** (Phytalmiinae: Acanthonevrini)**.** An endemic genus of two described species, *T. flaveolata* (F., 1805) (Fig. 24), distributed in East, Southern and West Africa and *T. rinhai* Korneyev, Hancock, Hauser, Korneyev & Gaimari, described from Madagascar (Korneyev *et al*. 2021). Several additional species were synonymised by Hancock (1986*a*). Larvae develop in the fruit of *Boscia caffra* Sond. and *Capparis erythrocarpa* Isert (Capparaceae). Biology and immature stages of the species otherwise remain unknown.

***Triandomelaena* Hancock** (Tephritinae: Pliomelaenini)**.** An endemic genus of three described species: *T. albina* (Bezzi, 1924) (Fig. 127), recorded from Kenya and Tanzania; *T. brevicostalis* Hancock, 1986 from Namibia and Zimbabwe; and *T. nigrofemorata* (Munro, 1929) from Namibia. Biology and immature stages remain unknown. No identification key to species is available, but *T. nigrofemorata* was discussed and transferred to this genus by Hancock (2006*a*). It is regarded as a close ally of *Pliomelaena*, differing in the abbreviated costal vein.

***Trirhithrum* Bezzi** (Dacinae: Ceratitidini)**.** An endemic genus of 40 described species (Figs 60–62) distributed in the continental Afrotropics and Indian Ocean islands. The widespread *T. nigerrimum* (Bezzi, 1913) is also known from the Comoros and *T. argenteocuneatum* Hancock, 1984 is known from Madagascar, Mauritius and Réunion Is., while four additional species are endemic to Madagascar. The Malagasy species, although not believed to form a monophyletic group, are unusual in having a metallic blue, green or purple sheen that might be associated with mimicry. Larvae develop in the flesh of small fruits and some are pests of coffee. Biology and immature stages otherwise remain unknown. White *et al*. (2003) provided a list of host-plants and an identification key to species.

***Trupanea* Schrank** (Tephritinae: Tephritini)**.** A virtually cosmopolitan genus of *ca* 220 described species, plus numerous undescribed species, occurring in all zoogeographical regions, except Antarctica. Some 48 species are known from the Afrotropics, including: *T. andobana* Munro, 1964 from Madagascar; *T. furcifera* Bezzi, 1924 from the continental Afrotropics and Madagascar; and *T. superdecora* Bezzi, 1924 from the continental Afrotropics, Mauritius and Réunion Is. Five largely Palaearctic species extend into the Arabian Peninsula: *T. amoena* (Frauenfeld, 1857) to United Arab Emirates and Palaearctic Saudi Arabia; *T. pseudoamoena* Freidberg, 1974 to Saudi Arabia; *T. pulcherrima* (Efflatoun, 1924) to Saudi Arabia and United Arab Emirates; *T. repleta* Bezzi, 1918 to Saudi Arabia and Yemen; and *T. stellata* (Fuesslin, 1775) to United Arab Emirates. The Kenyan species, *T. ornum* Norrbom, 1999 (formerly *T. mutabilis* Munro, 1964), also occurs in Yemen and a possibly undescribed species is known from Palaearctic Saudi Arabia (Merz & Dawah 2005). Larvae develop in flower heads or stems of a wide range of Asteraceae. Biology and immature stages otherwise remain unknown. Munro (1964) provided an identification key to Afrotropical species.

***Trupanodesis* Merz** (Tephritinae: Tephritini)**.** An endemic genus, with the single described species, *T. aurea* (Bezzi, 1924) (Fig. 175), recorded from Ethiopia to South Africa, plus an additional undescribed species known from Kenya and possibly Palaearctic Saudi Arabia (Merz 1999: 650; Merz & Dawah 2005). Larvae develop in flower heads of *Vernonia* (Asteraceae: Vernonieae). Biology and immature stages otherwise remain unknown.

***Trypanophion* Bezzi** (Trypetinae: Adramini)**.** An endemic monotypic genus, with the single described species, *T. gigas* Bezzi, 1924 (Fig. 32), recorded from Cameroon, Kenya, Malawi, Uganda and Zimbabwe. A second described species was synonymised by Hancock (1986*a*). Biology and immature stages of the species remain unknown.

Undescribed genus A (Tephritinae: Pliomelaenini)**.** An endemic monotypic genus with a single undescribed species (Fig. 129), recorded from Kenya. Biology and immature stages remain unknown.

Undescribed genus B (Tephritinae: Pliomelaenini)**.** An endemic monotypic genus with a single undescribed species (Fig. 130), recorded from Cameroon. Biology and immature stages remain unknown.

Undescribed genus C (Tephritinae: Tephritini)**.** An endemic monotypic genus with a single undescribed species (Fig. 144), recorded from Madagascar. Vein R_1 has a bare, non-setose area on the upperside, below the end of the subcostal vein (*Sc*) and

there is a broad, dark medial band in costal cell (c). Biology and immature stages remain unknown.

***Urophora* Robineau-Desvoidy** (Tephritinae: Myopitini)**.** A genus of 57 described and at least five undescribed species, occurring in the Afrotropical, Nearctic, Oriental and Palaearctic Regions. Several species have been introduced to the Nearctic and Oriental Regions for weed biocontrol. An undescribed species (Fig. 74), is known from Cameroon, reared from *Centaurea* (Asteraceae). Larvae develop mostly in flower head galls on various genera of Asteraceae (Carduaeae). Biology and immature stages otherwise remain unknown.

***Xanthanomoea* Bezzi** (Trypetinae: Rivelliomimini)**.** An endemic monotypic genus, with the single described species, *X. munroi* Bezzi, 1924 (Fig. 42), known only from South Africa and possibly Nigeria. Biology and immature stages of the species remain unknown.

***Xanthorrachista* Hendel** (Dacinae: Ceratitidini)**.** An endemic monotypic genus, with the single described species, *X. alata* (Becker, 1909) (Fig. 63), recorded from Democratic Republic of Congo and Kenya. Larvae develop in the fruit of Solanaceae. Biology and immature stages of the species otherwise remain unknown.

***Xenodorella* Munro** (Tephritinae: Pliomelaenini)**.** An endemic monotypic genus, with the single described species, *X. mira* Munro, 1967 (Figs 9, 128), known only from western Namibia. *Xenodorella* appears to be most closely related to *Deroparia* and *Euryphalara* (Hancock 2000). The larval host is not confirmed, but adults have been swept from *Monechma* (Acanthaceae), which is a likely host-plant. Biology and immature stages otherwise remain unknown.

***Ypsilomena* Munro** (Tephritinae: Tephrellini)**.** An endemic monotypic genus, with the single described species, *Y. compacta* (Bezzi, 1924) (Fig. 105), recorded from Kenya, Namibia, South Africa and Zimbabwe. Larvae develop in flower heads of *Leonotis* (Lamiaceae). Biology and immature stages of the species otherwise remain unknown.

***Zacerata* Coquillett** (Tephritinae: Zaceratini)**.** An endemic monotypic genus, with the single described species, *Z. asparagi* (Fig. 68), recorded from South Africa, Tanzania and possibly Angola. Larvae tunnel in the stems of *Asparagus* (Liliaceae) and pupariate within the hollowed-out stem. It was illustrated by Hancock (1986*a*), but the spermathecae are very weakly developed and it is likely that only two are present, not the three illustrated.

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PYRGOTIDAE 72

(Pyrgotid Flies or Scarab-killing Flies)

Valery A. Korneyev

Fig. 72.1. Male of *Campylocera angustigenis* Hendel (South Africa) (photograph © S.A. Marshall).

Diagnosis

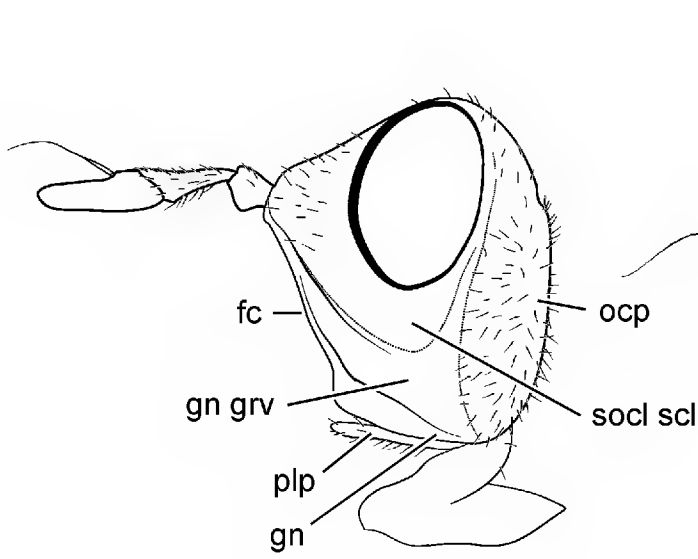
Medium-sized (body length: 3–18 mm), often slender acalyptrate flies, with long legs (Figs 1, 32–35); wing 3–20 mm in length, membrane hyaline with greyish tinge, often with banded or reticulated pattern (Figs 44–57) and mostly without frontal setae and ocelli.

Head (Figs 2–25) large, often with receding face and bulged occiput (Figs 2–13); ocelli absent in all Afrotropical species; face either with strong median facial carina (Figs 15–22) or entirely sunken (Figs 23–25); epistoma (= supraclypeal sclerite *sensu* Korneyev 2012), pentagonal or triangular (Figs 15–22), absent in *Toxopyrgota* Hendel (Fig. 14); subocular sclerite, a dilation of parafacial below ventral margin of compound eye, separated from gena and occiput by soft, non-sclerotised area, subdivided into genal groove and narrow postocular groove (latter apparently universal in all Pyrgotidae); mouthparts with small prementum and usually moderately developed labellum (very large in *Siridapha* Enderlein, Fig. 10, conspicuously reduced in *Toxopyrgota*, Fig. 13); palpus sometimes short, spatulate (Fig. 5) or elongate, narrow (Figs 2, 3); chaetotaxy variable; vibrissa absent; frontal setae reduced, except in *Toxopyrgota* (Fig. 13); orbital setae mostly proclinate (Fig. 13); outer vertical seta often reduced or absent (Figs 4, 6); ocellar and postocellar setae commonly well-developed (Fig. 13); antenna variable, from short (Fig. 5) to long (Fig. 6); antennal pedicel without dorsal notch or incision in Afrotropical species (except *Toxopyrgota*); postpedicel oval, short (Fig. 5) to very long (Fig. 6); with 2- or 3-articled, short-pubescent sub-basal arista.

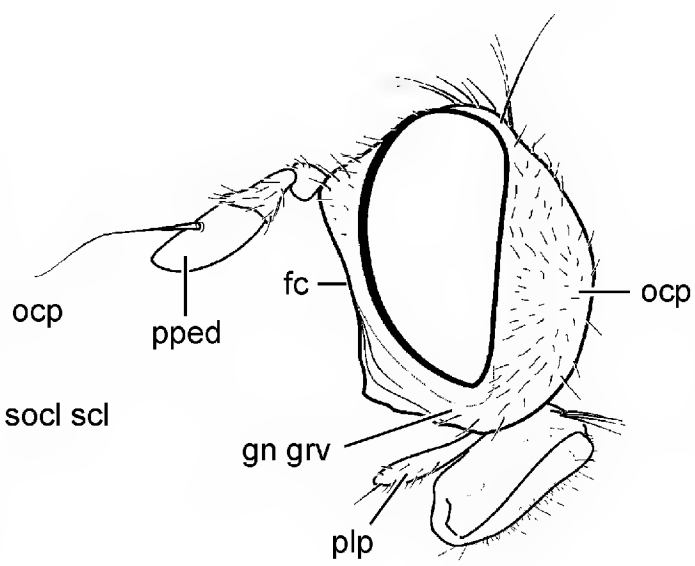
Thorax (Figs 26–29) sub-rectangular; chaetotaxy variable; commonly 1 postpronotal, 2 notopleural, 0 presutural and 1 postsutural supra-alar, 1 postsutural intra-alar, 1 postalar and 1 or 2 postsutural dorsocentral setae present (Figs 28, 29); in *Geloemyia* Hendel, also 1 presutural supra-alar, 3–4 dorsocentral and 1 prescutellar acrostichal setae present (Fig. 26); proepisternum, anepisternum, katepisternum and anepimeron

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2021. Manual of Afrotropical Diptera. Volume 3. Brachycera—Cyclorrhapha, excluding Calyptratae. *Suricata* 8. South African National Biodiversity Institute, Pretoria; pp. 1735–1751.

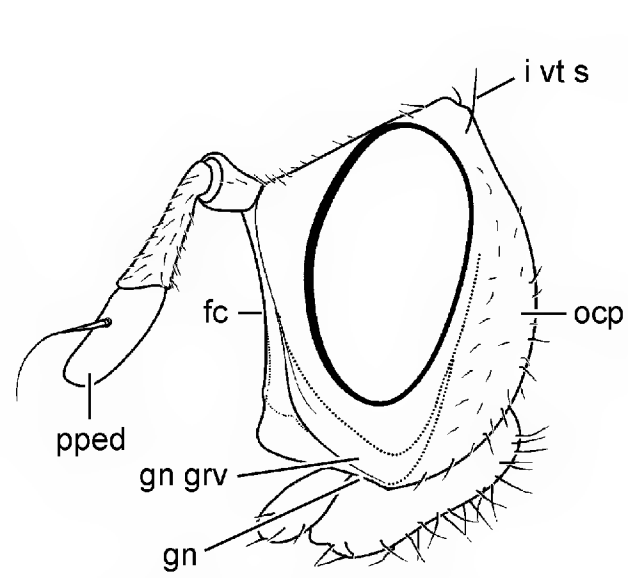
setulose, normally with strong setae; greater ampulla not expressed. Scutellum (Figs 26–29) usually short and wide, with 1–7 pairs of marginal scutellar setae (Figs 26–28); scutellar disc often setulose (Fig. 29). Wing (Figs 44–57) elongate, with venation similar to that of Tephritidae (see Chapter 71), except for subcostal vein (*Sc*); costal vein (*C*) with humeral weakening in Afrotropical species, without (or with inconspicuous) subcostal break; subcostal vein (*Sc*) complete, almost straight in Afrotropical species; vein R_1 dorsally setulose for entire length; vein R_{2+3} often with preapical auxiliary vein (Figs 33, 52, 53, 56, 57), secondarily lost in most *Tephritopyrgota* Hendel (Figs 44–48) and *Campylocera* Macquart (Figs 54, 55); posteroapical corner of cell *cua* with short triangular lobe (Fig. 47), or rarely closed by arcuate or straight vein (Fig. 50); alula and calypteres well-developed in Afrotropical species; wing membrane pattern variable, from entirely brown (Fig. 44), yellow (Fig. 45) or hyaline (Fig. 1), to reticulate (Figs 48, 49, 53), banded (Figs 47, 52), or partly hyaline, with extensive solid brown areas (Figs 55, 57); calypteres short; upper calypter in *Siridapha* with strong cilia (Fig. 36); halter in *Toxopyrgota* with conspicuously setulose stem, otherwise unmodified. Legs moderately developed or long (in *Siridapha*); mid and hind coxae of females sometimes with stiff setulae, often forming dense brushes (Fig. 43); in males, these setulae shorter, less thickened; mid coxal prong weak or reduced in some genera; fore and mid trochanters of *Eupyrgota* Coquillett with brushes of short spine-like setae (Fig. 42); hind coxa and trochanter in females of some *Campylocera* with soft flattened areas, possibly functioning as suckers; femora often with 2 rows of ventral setae; basalmost seta in posteroventral row on femora usually longer and thinner than others (Figs 38, 39); in males of *Toxopyrgota*, hind coxa and trochanter strongly modified, with additional lobes clothed in dense tuft of setulae (Fig. 37); mid femur in *Adapsilia* Waga, *Eupyrgota*, *Geloemyia* and *Siridapha* females sometimes with bare, poorly sclerotised area, the so-called "femoral organ" (Figs 38, 39, 40), or otherwise with trichose field (believed to serve hearing function); tibiae without long outstanding setae, except fore tibia sometimes with slightly thickened sub-erect apicodorsal setula and mid tibia with 2–3 black apicoventral setae; hind tibia usually constricted in basal ⅓, club-like (Fig. 41); anteroventral surface of tibiae in females commonly with thick brush of appressed yellowish setulae; female fore tarsi sometimes with long and curled setulae and hind tarsomeres 1–4 often asymmetrical, with comb of setulae



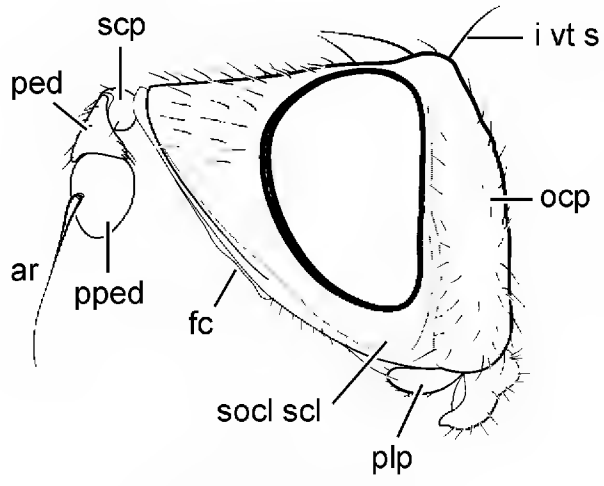
2 *Campylocera*



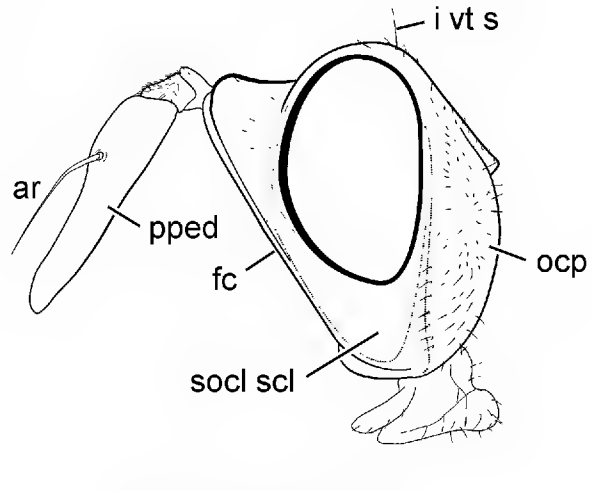
3 *Campylocera*



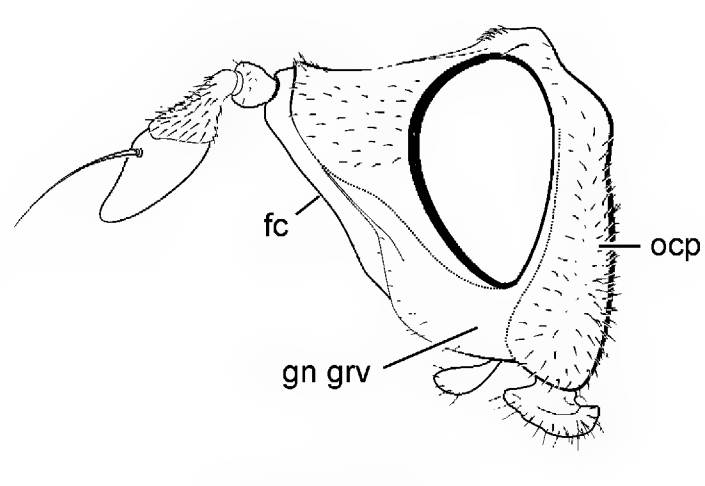
4 *Eupyrgota* (*Eupyrgota*)



5 *Geloemyia*



6 *Hendelpyrgota*



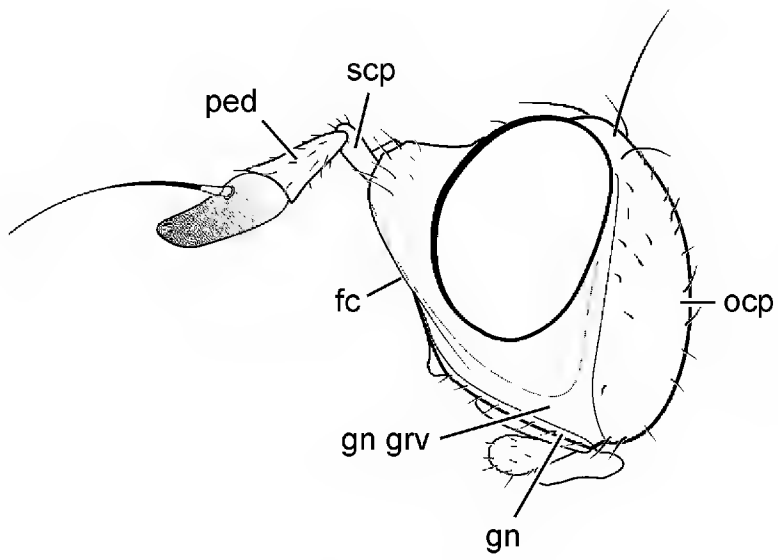
7 *Pyrgotina*

Figs 72.2–7. Heads of Pyrgotidae (lateral views): (2) *Campylocera laticeps* (Hendel); (3) *C. ferruginea* (Macquart); (4) *Eupyrgota* (*Eupyrgota*) *vespiformis* (Enderlein); (5) *Geloemyia namibiensis* Korneyev; (6) *Hendelpyrgota longicornis* Vanschuytbroeck; (7) *Pyrgotina tipuloides* (Hendel).

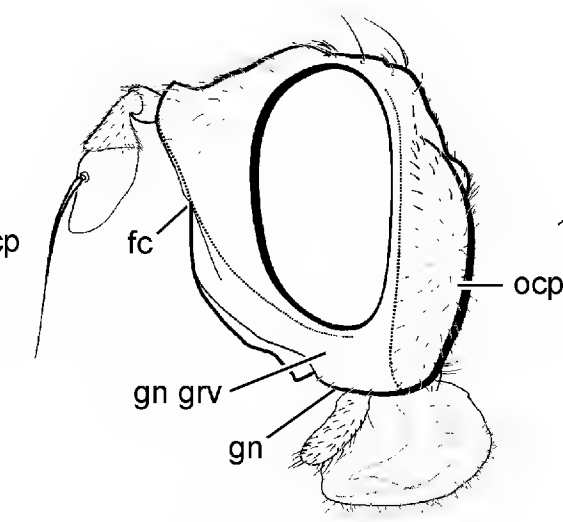
Abbreviations: ar – arista; fc – face; gn – gena; gn grv – genal groove; i vt s – inner vertical seta; ocp – occiput; ped – pedicel; plp – palpus; pped – postpedicel; scp – scape; socl scl – subocular sclerite.

on anteroventral surface; claws and pulvilli of females in Afrotropical species sometimes enlarged (Fig. 37); many of these modifications of legs in females present only in species with ventrally curved oviscape and believed to be adaptations for firm attachment to their hosts during oviposition.

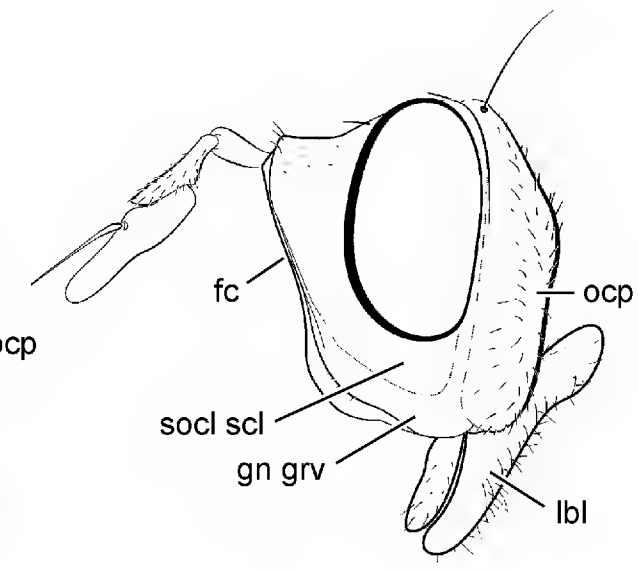
Abdomen with sternites 1 and 2 fused in all Afrotropical species; in *Eupyrgota* and *Siridapha*, syntergite and synsternite 1 + 2 long, in males conspicuously longer than in females (Figs 69, 70), especially in species with long female oviscape, apparently to make copulation possible; female sternites usually setulose; in some non-Afrotropical species bare, almost smooth, with cellular micro-sculpture, or alternately, with dense stiff setae (Fig. 72); female tergites and sternites 5 and 6 very often short, transverse; sternites 4–6 with short, sometimes poorly visible, medioventral apodemes (Fig. 71); oviscape (female tergosternite 7) usually as long as or longer than preabdomen (Figs 32–34); male terminalia, as in other "higher Tephritoidea" (*sensu* Korneyev 1999: 10), with bare sternites 6 and 7, without spiracles 6 and 7 (Fig. 69); male terminalia with hypandrium symmetrical; phallapodeme with long separate vanes (paired processes) joined to bare and subequal, bar-like pregonites in *Toxopyrgota* (Figs 58, 60), or to hypandrium in its anterior ½, rather than to virtually absent pregonites (Figs 62, 66–68); posterior part of hypandrium in almost all Pyrgotinae with 2 flaps, clothed in scales or microtrichia forming phallic guide (Fig. 66); pair of sensillar fields, round sclerites bearing 7–8 trichoid sensilla usually present in posterior portion at margins of basiphallus (Fig. 66); phallus consisting of short, ring-like basiphallus (Fig. 58) and long and coiled distiphallus (Fig. 58), in Afrotropical, Oriental and Holarctic species somewhat simplified and de-sclerotised with apical glans (Figs 61, 64), as compared to a few early branching Nearctic and Australasian forms, more similar to those in Tephritidae; sperm pump with moderately large round sack and elongate fan-like ejaculatory apodeme (as in Tephritidae); epandrium setose in *Toxopyrgota* (Figs 58, 59), or almost entirely bare, except a few setulae at posterior margin lateral to cercus in other Afrotropical species



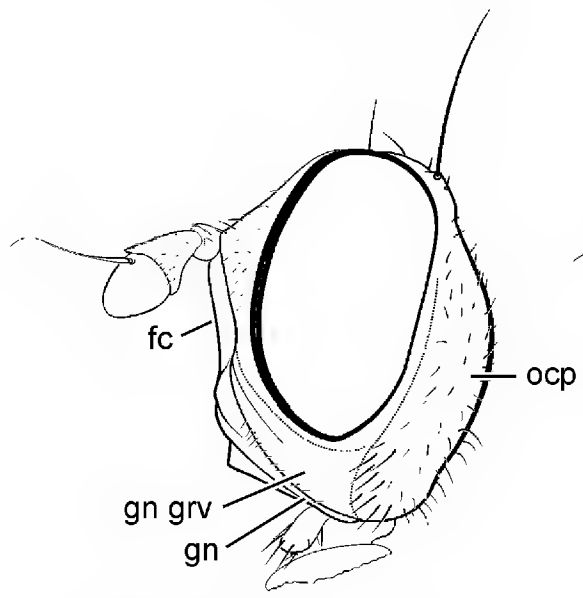
8 *Pyrgotomyia*



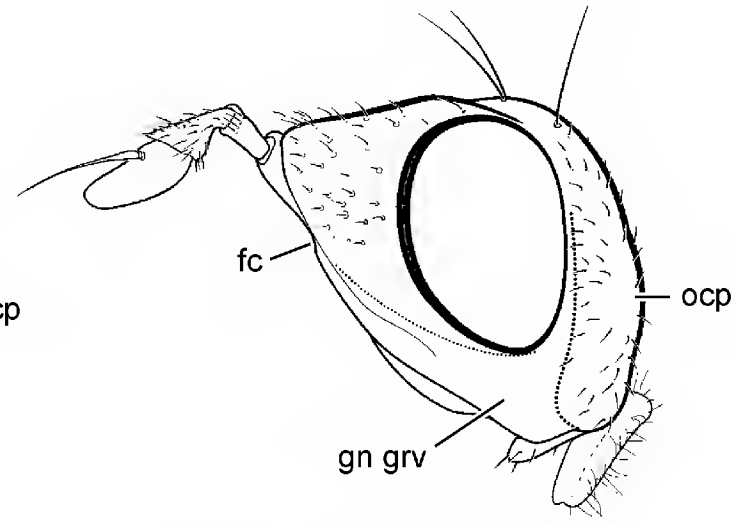
9 *Rhagostira*



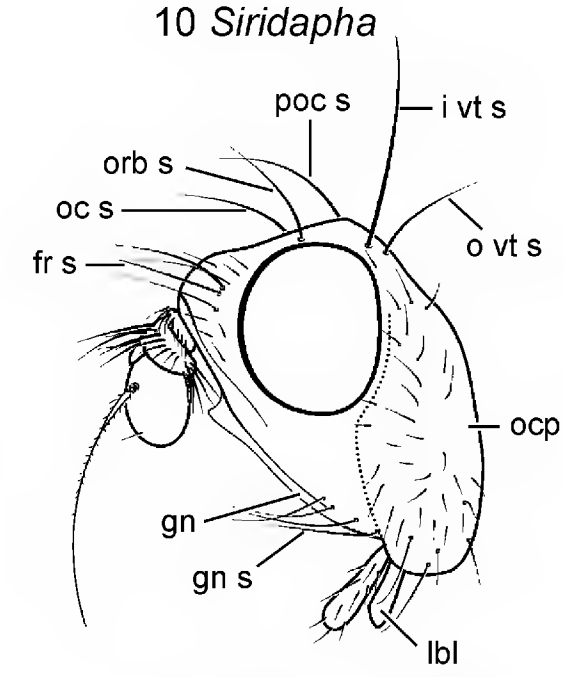
10 *Siridapha*



11 *Tephritopyrgota*



12 *Tephritopyrgota*

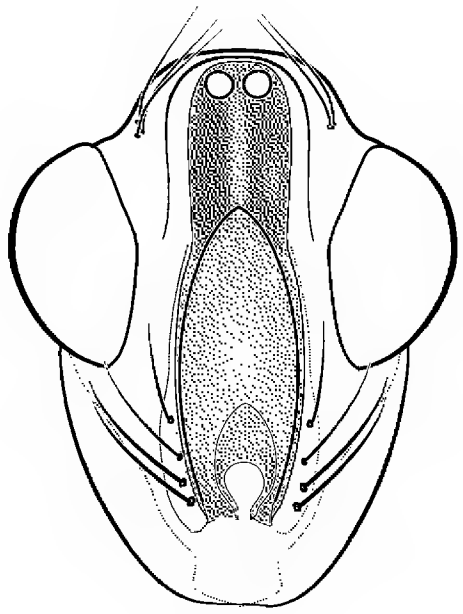


13 *Toxopyrgota*

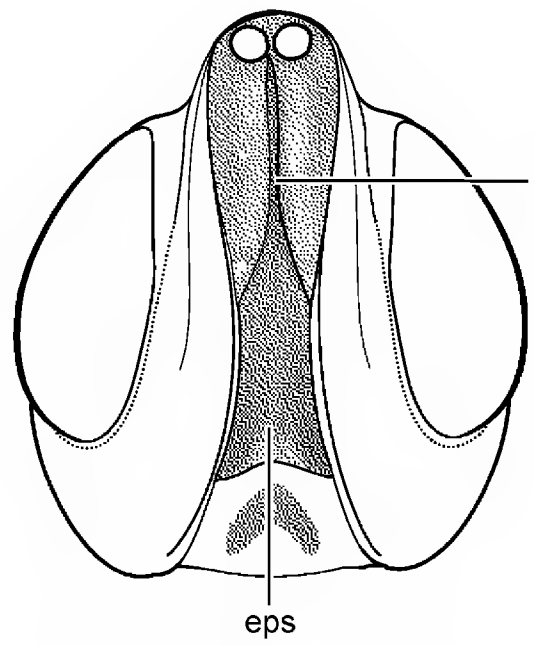
Figs 72.8–13. Heads of Pyrgotidae (lateral views): (8) *Pyrgotomyia ciliata* Hendel; (9) *Rhagostira* sp.; (10) *Siridapha mulguensis* (Vanschuytbroeck); (11) *Tephritopyrgota gowdeyi* Malloch; (12) *Te. tenuis* Hendel; (13) *Toxopyrgota inclinata* Hendel.

Abbreviations: fc – face; fr s – frontal seta; gn – gena; gn grv – genal groove; gn s – genal seta; i vt s – inner vertical seta; lbl – labellum; o vt s – outer vertical seta; oc s – ocellar seta; ocp – occiput; orb s – orbital seta; ped – pedicel; poc s – postocellar seta; scp – scape; socl scl – subocular sclerite.

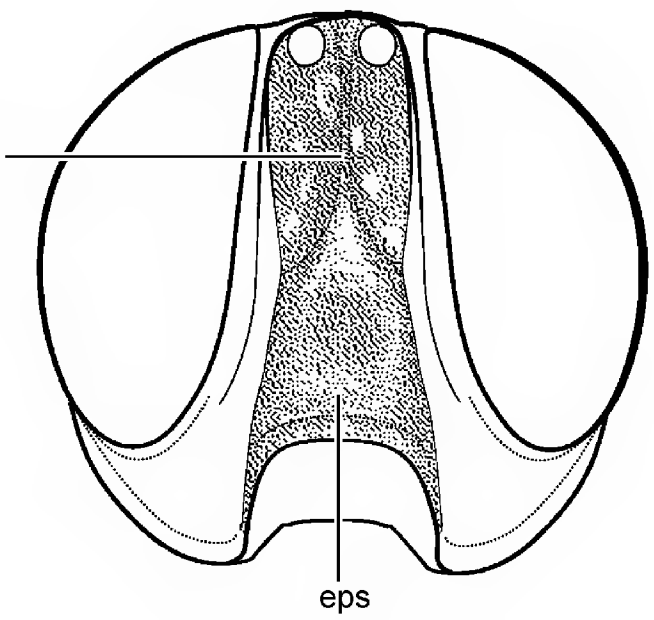
(Figs 62, 68); inner (medial) surstylus simple, with short setulae; 2 prensisetae, similar to those in Tephritidae, present in some Nearctic and Australasian species and 1 prensiseta in *Toxopyrgota* (Fig. 59); in all other Afrotropical genera prensisetae absent (Figs 62, 63, 68, 69); outer (lateral) surstylus usually microtrichose and papillose (Figs 62, 68), short in most *Campylocera*, *Eupyrgota* (subgenus *Taeniomastix* Enderlein) and *Adapsilia*, sometimes bilobate (Fig. 62), elongate in *Geloemyia*, *Eupyrgota sensu stricto* and *Tephritopyrgota* (Fig. 67), or very long in *Siridapha* (Fig. 68); cercus simple, often enlarged (Figs 62, 63), with clear ventromedial weakening, or in some *Tephritopyrgota* and Oriental *Plectrobrachis* Enderlein, bilobate; female terminalia (Figs 73, 75) in general similar to those of Tephritidae (see Chapter 71); tergosternite 7 in all Afrotropical species forming conical oviscape, apically with variously arranged fields of setulae or trichoid sensilla, often bearing special sclerotic structures, such as single ventral claw (in *Pyrgotina* Malloch and *Tephritopyrgota*), fields of spinulose setulae (some *Campylocera* and *Eupyrgota*), row of stiff, basally fused medioventral setae (Australian *Prodalmannia* Bezzi), or paired sclerotised hooks (ovipositungui) (*Eupyrgota*) (Figs 73, 74), or axe-like, rounded medial blade (in some *Campylocera*); anteroventral portion of oviscape with large, flap-like apodeme, enabling closure of anterior aperture entirely to create high pressure of hemolymph within oviscape; in some *Siridapha* ventral surface of oviscape with sucker-like groove (Fig. 76); eversible membrane thick, but devoid of scales or microtrichia in all Afrotropical species, often supported by sclerotised, spring-like medial or dorso- and ventrolateral lobes of oviscape; aculeus in Pyrgotidae usually short and simple, usually ½ as long as oviscape or much shorter (Figs 77, 79, 80), in some species moderately long (Fig. 78), bearing no large setae, with thin, inconspicuous ventral lobes, consisting mainly of entirely consolidated, blade-like cercal unit (cerci fused with remainders of segments 9 and 10) and wide basal portion corresponding to tergite 8; 3 (sometimes 2) oval or round, poorly sclerotised spermathecae with ducts separated from vagina, as in Tephritidae; ventral receptacle in Afrotropical species with long simple basal "neck" and round apical part.



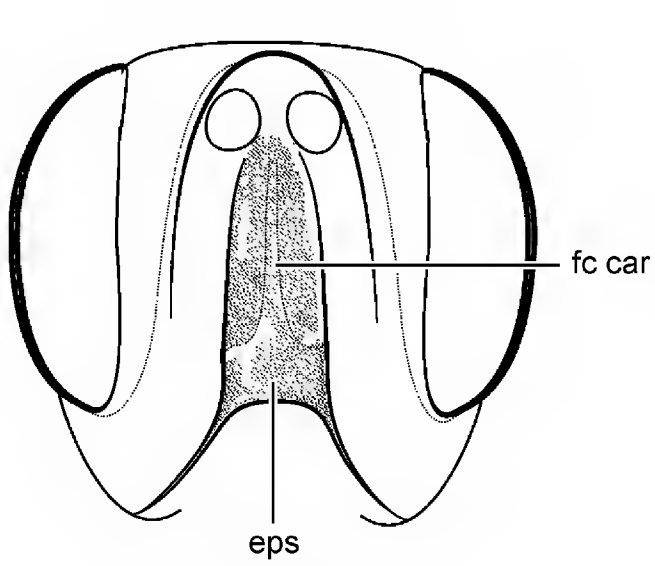
14 *Toxopyrgota*



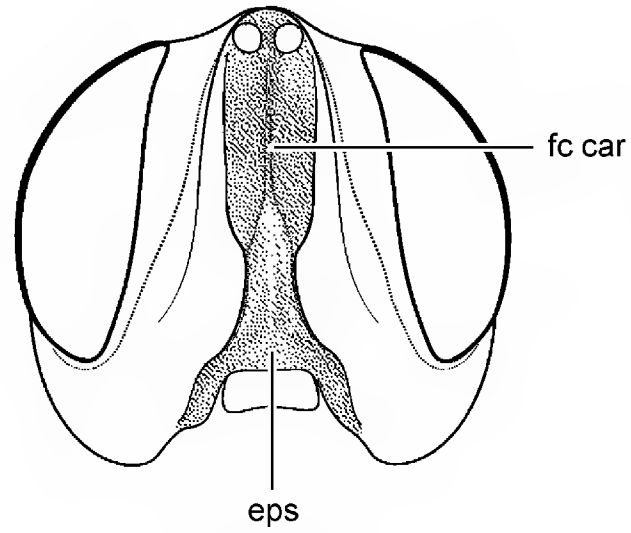
15 *Tephritopyrgota*



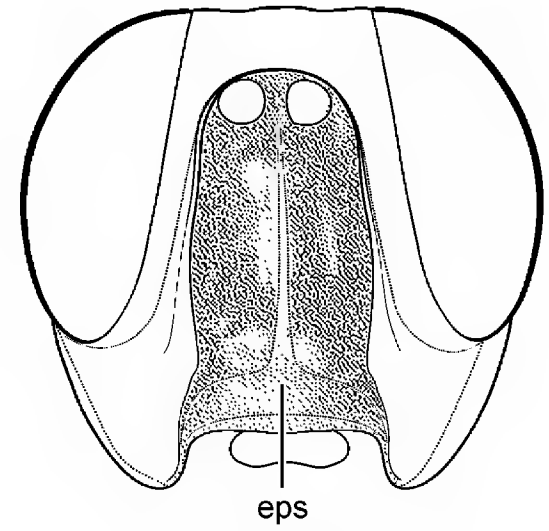
16 *Tephritopyrgota*



17 *Tephritopyrgota*



18 *Pyrgotina*



19 *Rhagostira*

Figs 72.14–19. Heads of Pyrgotidae (anterior views): (14) *Toxopyrgota inclinata* Hendel; (15) *Tephritopyrgota tenuis* Hendel; (16) *Te. binodosa* Hennig; (17) *Te. spinosa* Hennig; (18) *Pyrgotina tipuloides* (Hendel); (19) *Rhagostira* sp.

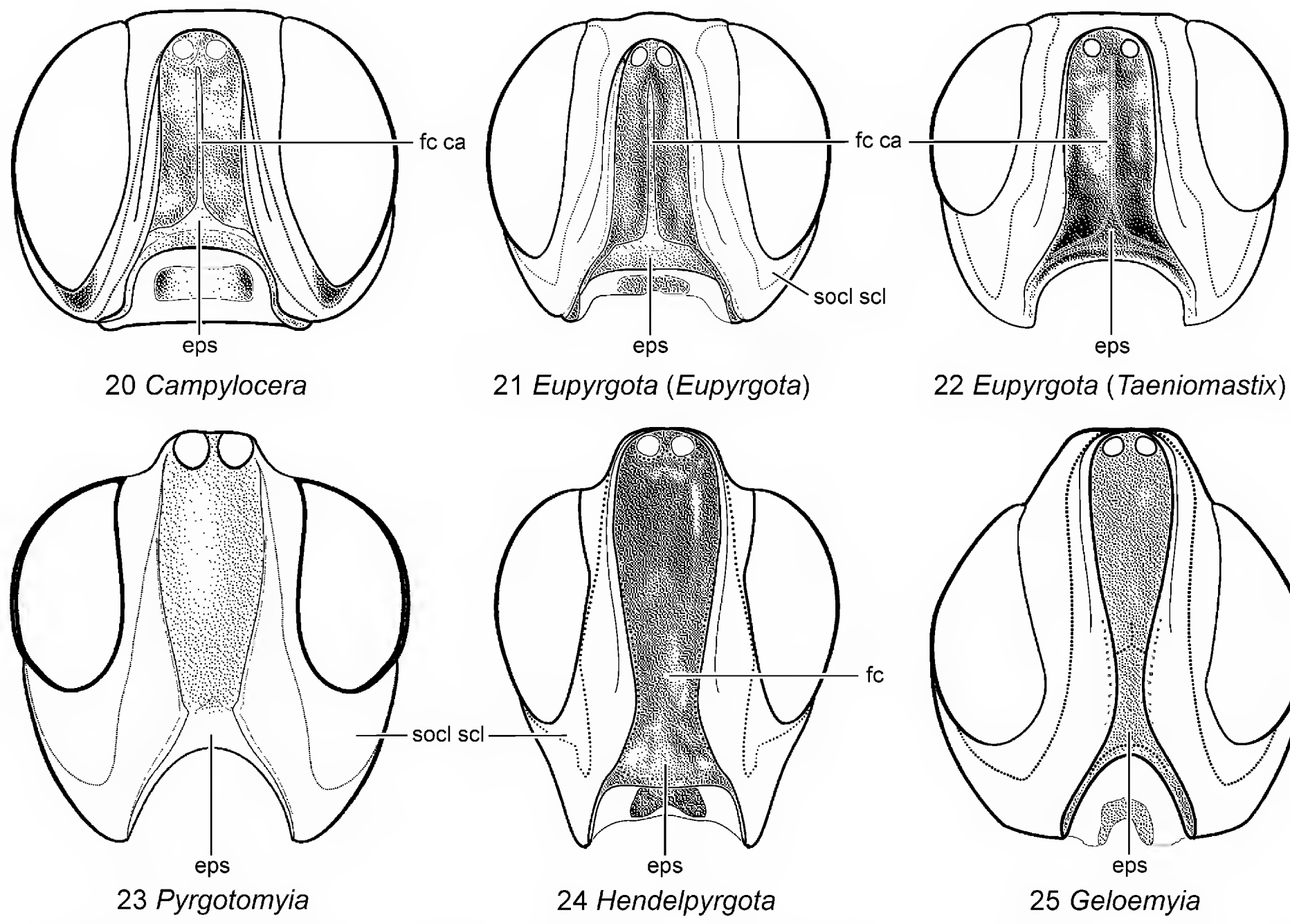
Abbreviations: eps – epistoma; fc car – facial carina.

Egg (Figs 81, 82) moderately elongate and bluntly rounded at micropilar end, more or less tapered to opposite end. Description and figures of larva and puparium only known for Nearctic *Pyrgota* Wiedemann and *Sphecomyiella* Hendel (Davis 1919) and for Oriental *Eupyrgota* (*Asiapyrgota*) *flaviseta* (Aldrich, 1928) (Clausen *et al*. 1933) (Figs 83–86). Larvae wide and short, tear-shaped, with cephaloskeleton (Figs 85, 86) similar to those in *Acanthonevra* Macquart (Tephritidae), but strongly widened laterally; heavily branched prothoracic spiracle (Fig. 83) and posterior spiracle of complex shape, with sclerotised posterodorsal projection (Fig. 84).

Afrotropical Pyrgotidae are usually wasp-like flies that superficially resemble some Tephritidae, especially representatives of the tribe Dacini, in having reddish yellow body colour, often with brown maculae and vittae and predominantly hyaline wings, but are readily distinguished from these by the absence of ocelli and the short triangular lobe of wing cell *cua*. A few Platystomatidae (*Bromophila* Loew) (see Chapter 70) and Tephritidae: Tachiniscinae (*Bibundia* Bischoff) (see Chapter 71), without ocelli and frontal setae, are robust black flies, either without the posteroapical lobe of cell *cua*, or with more than five pairs of marginal scutellar setae. Afrotropical *Toxopyrgota* that have 2–3 pairs of orbital setae and cell *cua* closed by the arcuate crossvein without posteroapical lobe, can be differentiated from both Tephritidae (frontal setae present) and Platystomatidae (cell *cua* without lobe), by the combination of ocelli lacking, but the ocellar setae long.

Biology and immature stages

Some species of Pyrgotidae are known to be parasitoids within the bodies of adult Coleoptera (*i.e.*, Scarabaeidae: Melolonthinae, Rutelinae and Cetoniinae). Adult Pyrgotidae are crepuscular, along with their hosts and are most frequently collected at mercury-vapour lights and in Malaise traps deployed overnight (A.H. Kirk-Spriggs, pers. comm. 2014). In some instances, adults have also been collected on flowers during daytime.



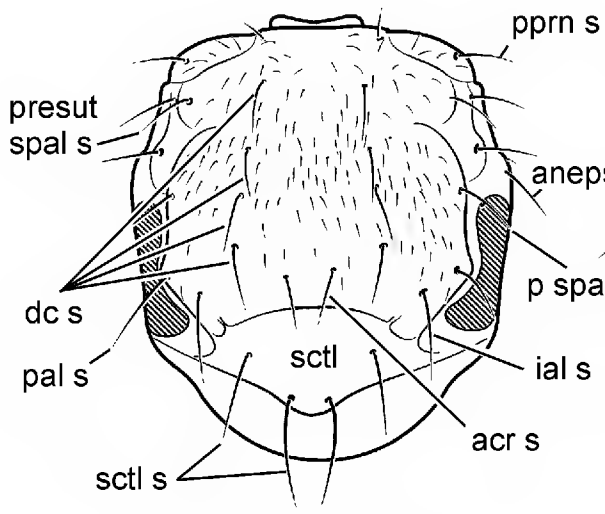
Figs 72.20–25. Heads of Pyrgotidae (anterior views): (20) *Campylocera ferruginea* (Macquart); (21) *Eupyrgota* (*Eupyrgota*) *latipennis* (Walker); (22) *E.* (*Taeniomastix*) *spinifemur* (Hendel); (23) *Pyrgotomyia temporalis* Steyskal; (24) *Hendelpyrgota longicornis* Vanschuytbroeck; (25) *Geloemyia namibiensis* Korneyev.

Abbreviations: eps – epistoma; fc – face; fc car – facial carina; socl scl – subocular sclerite.

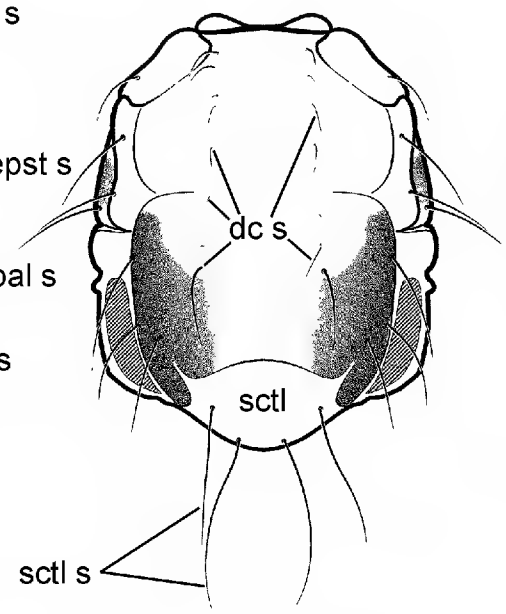
Forbes (1908) and Davis (1913, 1919) reported Nearctic *Pyrgota undata* (Wiedemann, 1830) and *Sphecomyiella valida* (Harris, 1841) to be reared from several species of *Phyllophaga* Harris (Coleoptera: Scarabaeidae: Melolonthinae) in North America. Female flies pierce the thin integument of the abdominal dorsum which is exposed as the beetle takes flight and larva develops solely in each host, killing the beetle within 10–14 days. Pupariation takes place, as in most species listed below, in the abdomen of the dead host.

Clausen *et al.* (1933) described the biology of *Eupyrgota* (*A.*) *flaviseta* (as *Adapsilia*) attacking a *Popillia* sp. (Coleoptera: Scarabaeidae: Rutelinae), principally males in India. *Campylocera hirsuta* Aldrich, 1928, was reared from an adult *Adoretus* sp. (Rutelinae) in Taiwan (Aldrich 1928); and *C. robusta* de Meijere, 1880, from *Adoretus compressus* (Weber, 1801) in Java, Indonesia (de Meijere 1916). These two nominal species of flies are believed to be synonyms (Korneyev, in prep.). Nartshuk & Korneyev (2005) recorded *Serica koltzei* Reitter, 1897 (Melolonthinae: Sericini) as a host of *Parageloemyia quadriseta* Hendel, 1908. Clausen (1940: 404) and Paramonov (1958a, *b*) noted the primitive Australian pyrgotids *Frontalia noctua* Paramonov, 1958 and *Prodalmannia variabilis* Bezzi, 1929, ovipositing on *Phyllotocus macleayi* Fischer, 1823 (Melolonthinae: Sericini) and *Maenomenus ensifer* Bezzi, 1929, pursuing a ruteline beetle, *Anoplognathus hirsutus* Burmeister, 1844, rising high on its legs and bending its long ovipositor beneath the thorax to oviposit through the anus of its potential host. Ten to twenty (rarely up to 33) larvae of *M. ensifer* develop in each beetle and larvae pupariate between the elytra and abdominal tergites (Burrell cited *in* Clausen 1940: 404). According to unpublished label data, Patagonian *Teretrura tinctipennis* Malloch, 1933 and *Pyrgotosoma flavida* Malloch, 1933 were both reared from *Sericoides obesa* (Fairmaire & Germain, 1863) (Melolonthinae: Sericini).

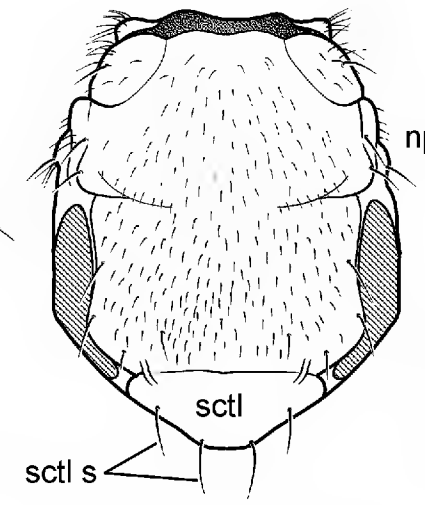
Thus far, the only Afrotropical pyrgotid reared from its hosts is *Eupyrgota* (*E.*) *latipennis* Walker, 1849, parasitising the abdomen of adult *Pachnoda interrupta* (Olivier, 1789) (Cetoniinae)



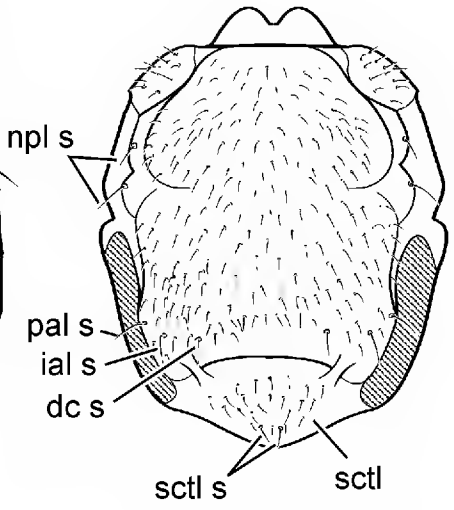
26 *Geloemyia*



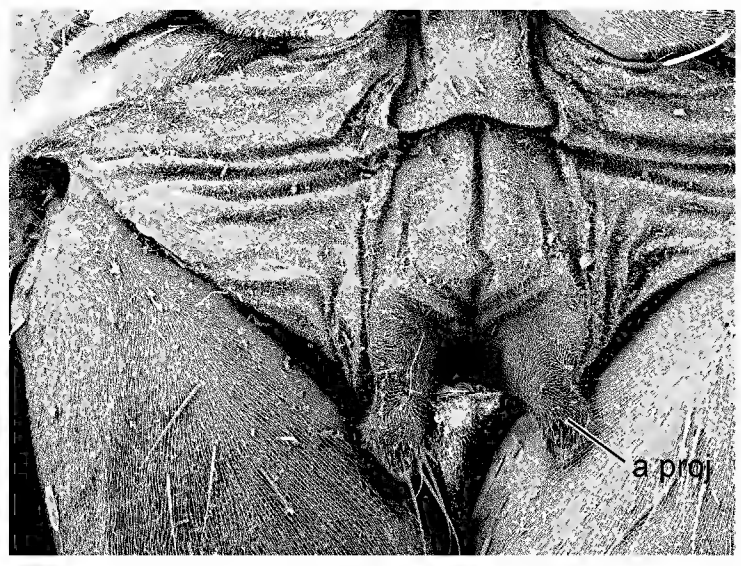
27 *Pyrgotomyia*



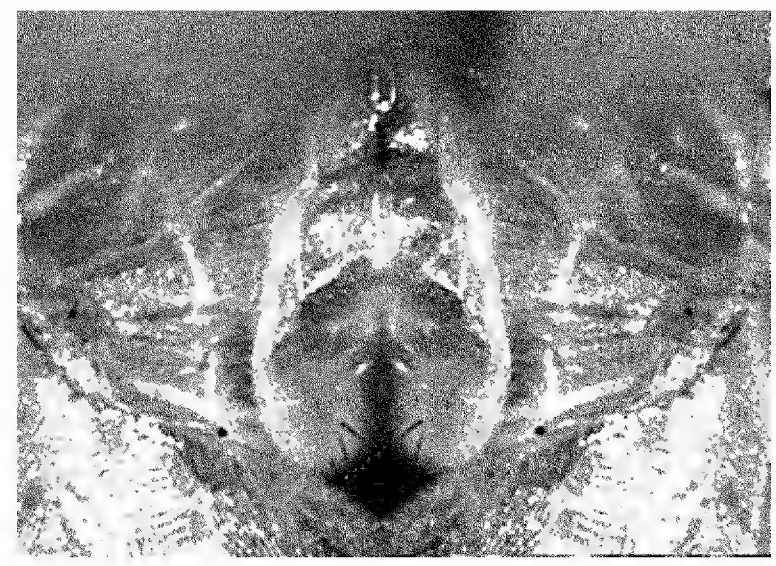
28 *Eupyrgota* (*Eupyrgota*)



29 *Pyrgotina*



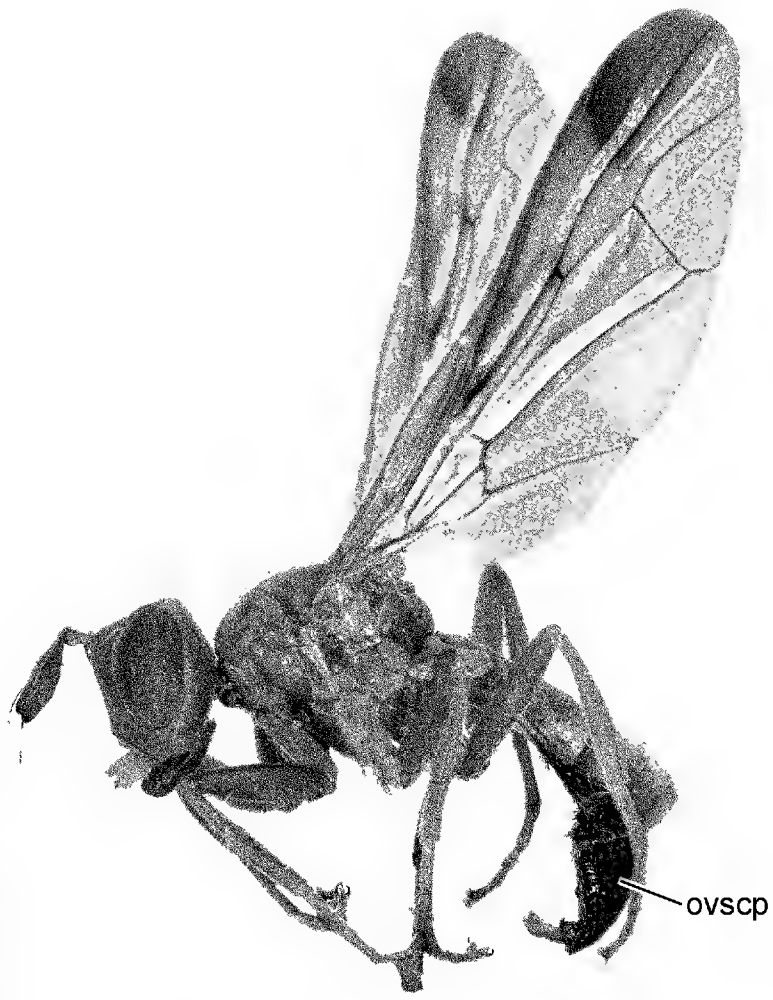
30 *Eupyrgota* (*Eupyrgota*)



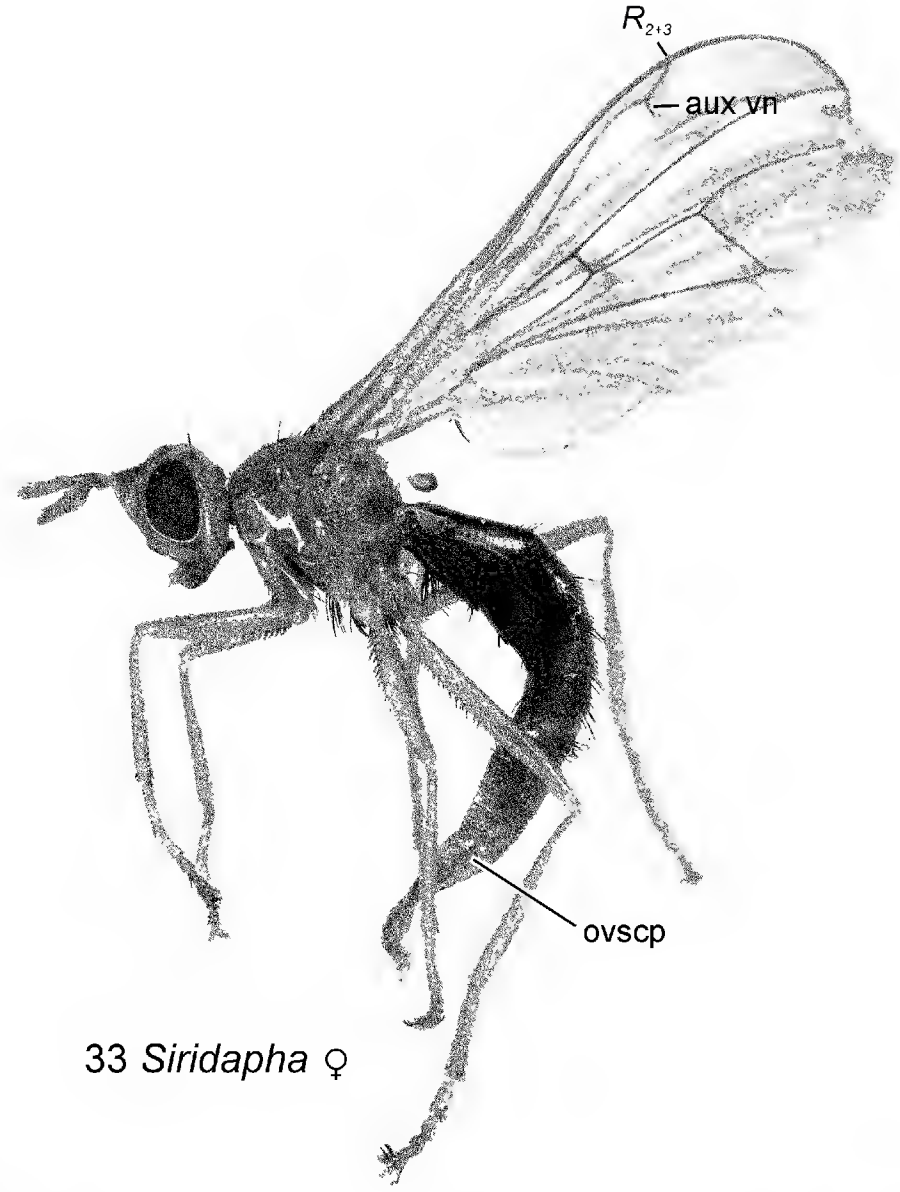
31 *Campylocera*

Figs 72.26–31. Mesonota and prosterna of Pyrgotidae: (26) mesonotum of *Geloemyia dorsocentralis* (Enderlein), dorsal view; (27) same, *Pyrgotomyia stuckenbergi* Korneyev; (28) same, *Eupyrgota* (*Eupyrgota*) *latipennis* (Walker); (29) same, *Pyrgotina tipuloides* (Hendel); (30) prosternum of *E.* (*E.*) *latipennis*, anterior view; (31) same, *Campylocera proxima* Séguy.

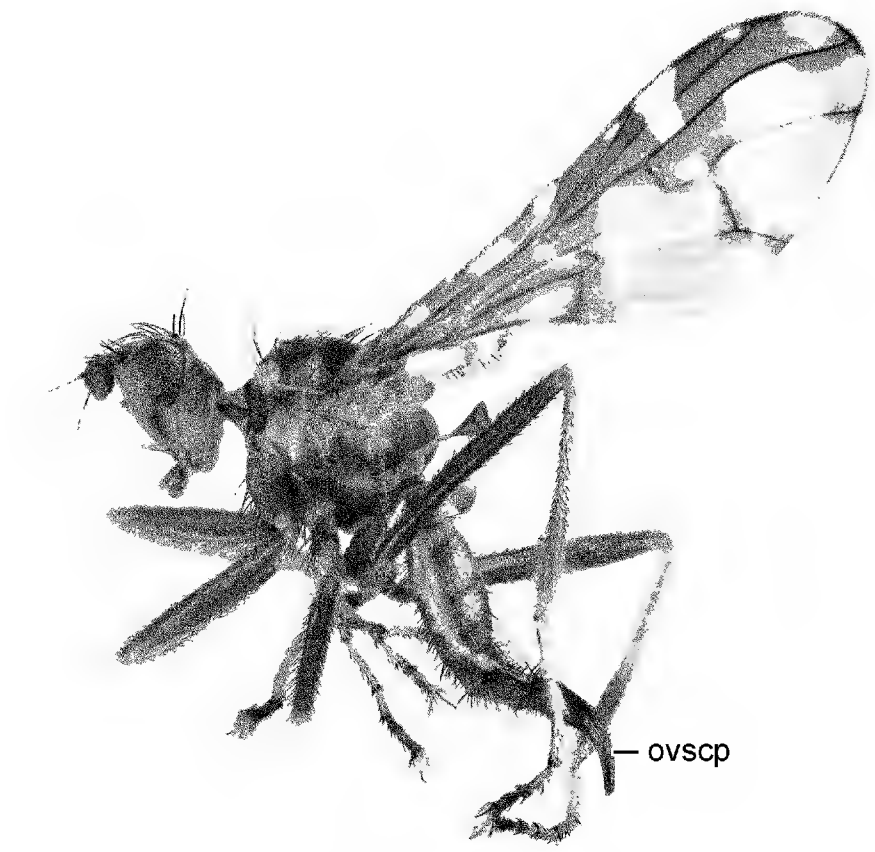
Abbreviations: a proj – apical projection; acr s – acrostichal seta; anepst s – anepisternal seta; dc s – dorsocentral seta; ial s – intra-alar seta; npl s – notopleural seta; p spal s – posterior supra-alar seta; pal s – postalar seta; pprn s – postpronotal seta; presut spal s – presutural supra-alar seta; s – setae; sctl – scutellum; sctl s – scutellar seta.



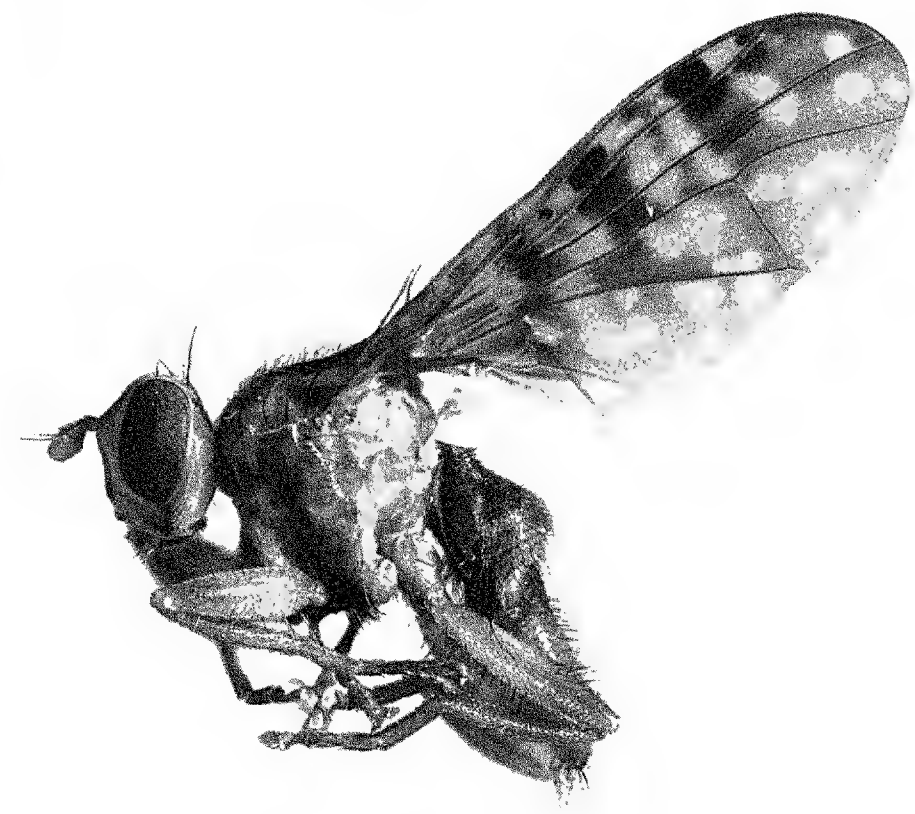
32 *Eupyrgota* (*Eupyrgota*) ♀



33 *Siridapha* ♀



34 *Toxopyrgota* ♀



35 *Tephritopyrgota* ♀

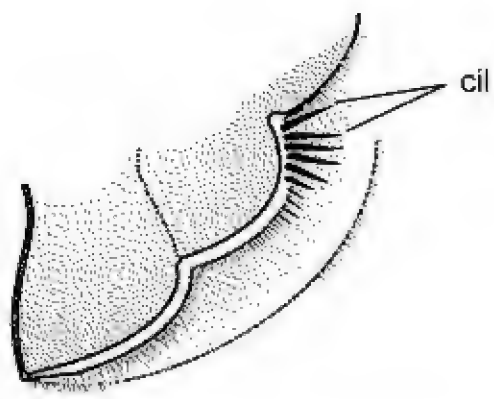
Figs 72.32–35. Habitus of female Pyrgotidae (lateral views): (32) *Eupyrgota* (*Eupyrgota*) *latipennis* (Walker); (33) *Siridapha* sp.; (34) *Toxopyrgota inclinata* Hendel; (35) *Tephritopyrgota gowdeyi* Malloch.

Abbreviations: aux vn – auxiliary vein; ovscp – oviscape; R_{2+3} – second branch of radius.

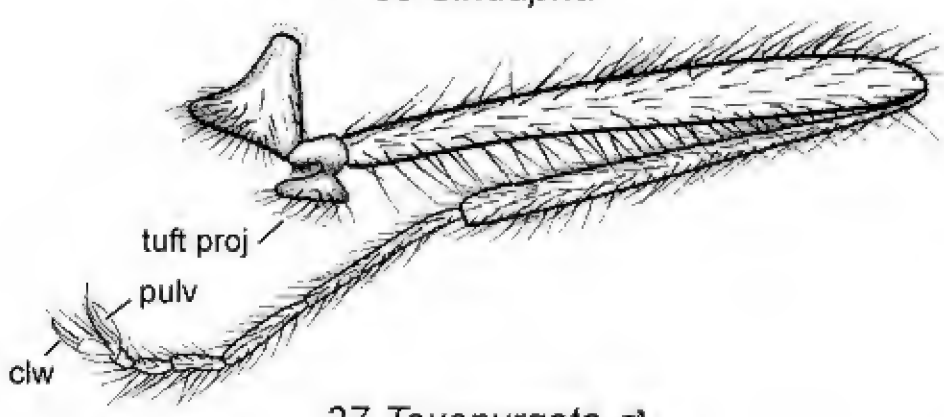
(Figs 88, 89) in Ethiopia (Korneyev 2006*b*). Previously, it was reported from South Africa as a parasite of *Hypopholis sommeri* Burmeister, 1855 (Hennig 1952), but this record is ascribable to another species, as *E.* (*E.*) *latipennis* does not occur there. A single tear-shaped puparium is enclosed in the beetle's abdomen with its posterior end upturned to the anterior end of the abdomen (Fig. 89).

Economic significance

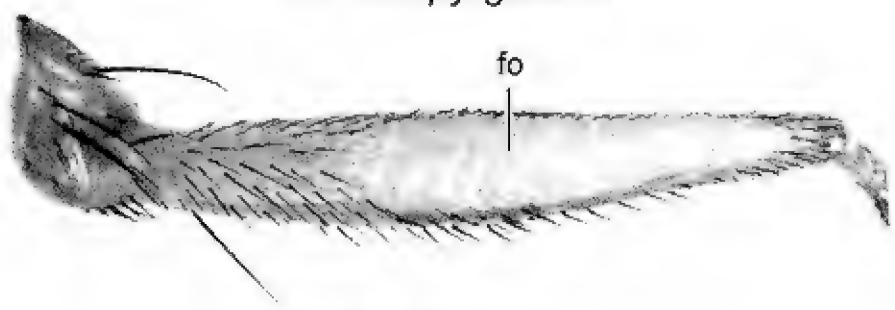
Afrotropical *Eupyrgota* (*E.*) *latipennis* parasitise adult *Pachnoda interrupta* (Scarabaeidae: Cetoniinae), a common pest of cultivated sorghum (Poaceae) in Ethiopia (Korneyev 2006*b*) and may regulate population of that species (see above). No other cases of economically important Pyrgotidae are recorded in the literature.



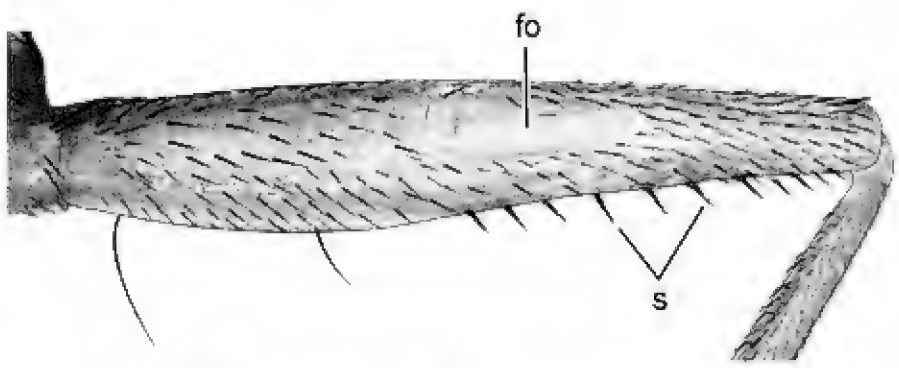
36 *Siridapha*



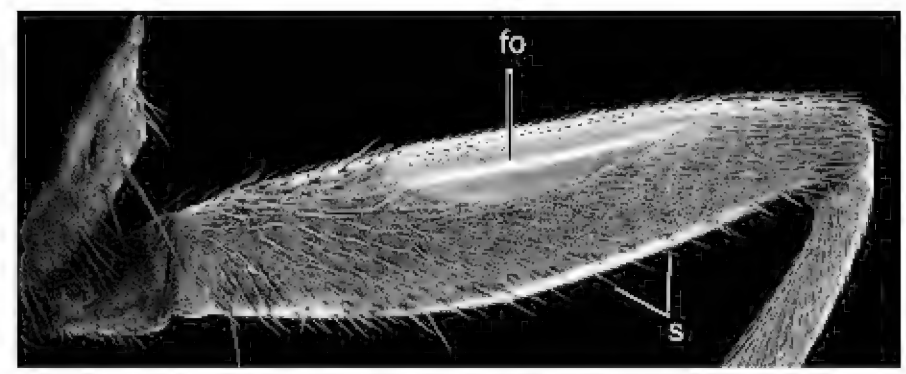
37 *Toxopyrgota* ♂



38 *Siridapha*

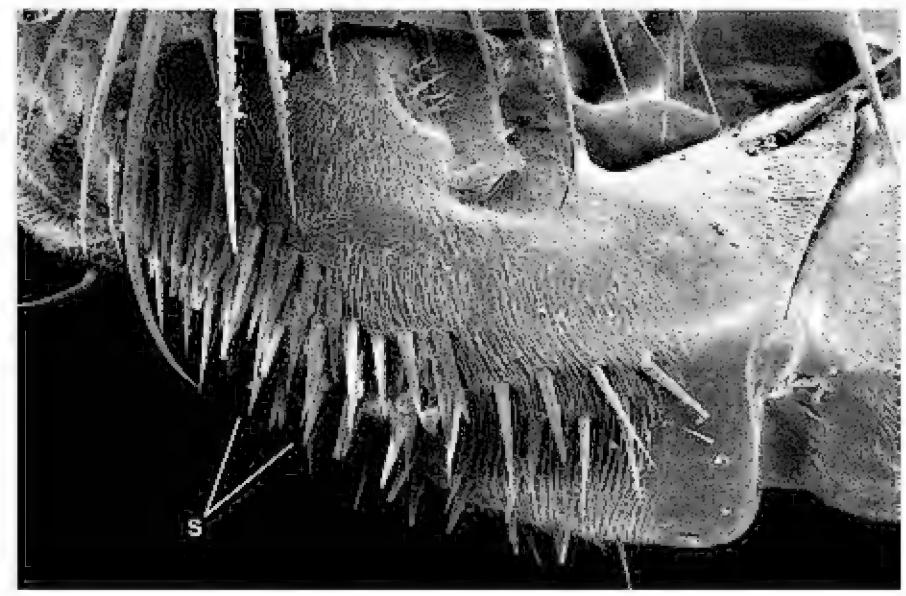


39 *Eupyrgota* (*Taeniomastix*)

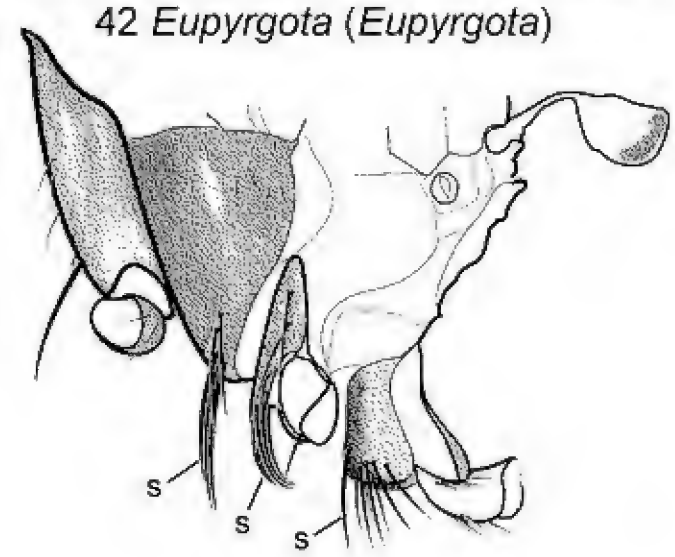


40 *Eupyrgota* (*Eupyrgota*)

41 *Pyrgotina*



42 *Eupyrgota* (*Eupyrgota*)



43 *Siridapha*

Figs 72.36–43. Calypter and legs of Pyrgotidae: (36) calypter of *Siridapha* sp., dorsal view; (37) male hind leg of *Toxopyrgota inclinata* Hendel, anterior view; (38) mid coxa, trochanter and femur of *Siridapha* sp., anterior view; (39) same, *Eupyrgota* (*Taeniomastix*) *spinifemur* (Hendel); (40) same, *E.* (*E.*) *caffra* (Hendel); (41) hind tibia of *Pyrgotina tipuloides* (Hendel), lateral view; (42) fore trochanter of *E.* (*E.*) *caffra*, ventral view; (43) coxae and trochanters of *Siridapha* sp., lateral view.

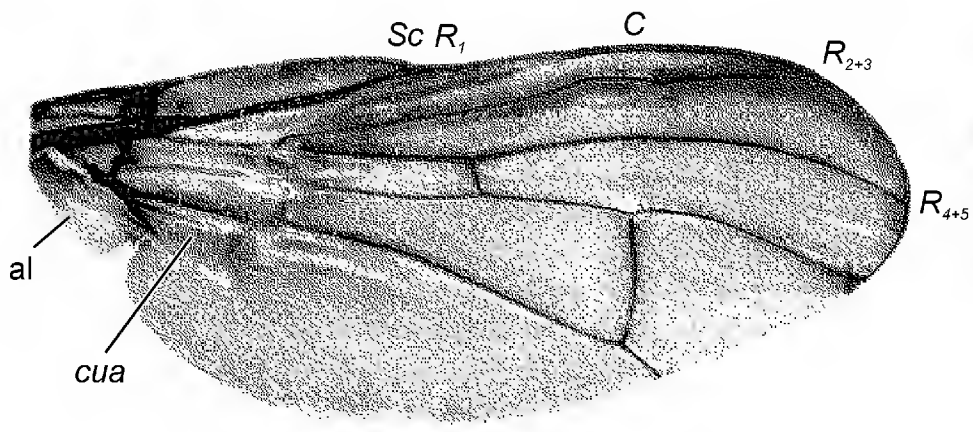
Abbreviations: cil – cilia; clw – claw; cx – coxa; fo – femoral organ; pulv – pulvillus; s – setae; tuft proj – tufted projection.

Classification

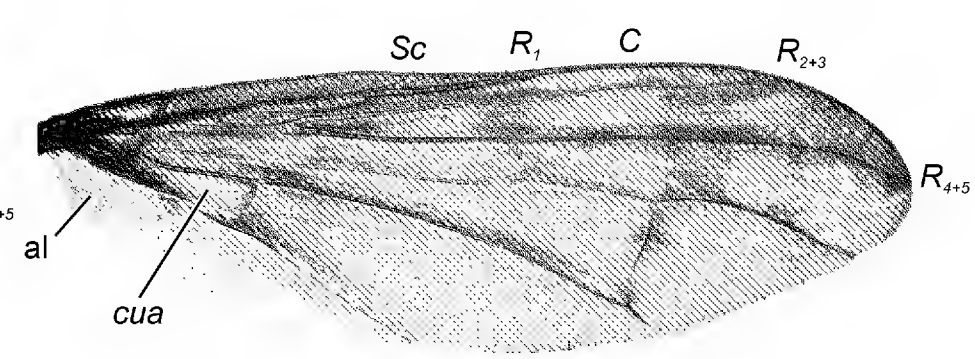
Pyrgotidae are closely related to Tephritidae (including Tachiniscinae), sharing at least one synapomorphy: 3 separated spermathecal ducts (in other Tephritoidea, 1 of the 2 spermathecal ducts is Y- or T-shaped and bifurcated at its apex).

The monophyly of Pyrgotidae is poorly supported by having a solid aculeus with the cerci entirely fused with segment 8, believed to be an adaptation for oviposition into the bodies of adult beetles. Similar modifications are, however, also common in the Tachiniscinae (parasitoids of caterpillars) and many other tephritids ovipositing into live plant tissues. The presence of a poorly sclerotised postocular groove (that apparently allows deep articulation of the face and inflation of a very large ptilinum to eclose from the beetle's body), appears to be primarily present in all Pyrgotidae lineages and also in *Nosferatumyia* Korneyev, *Descoleia* Aczél (family position uncertain) and *Aliasutra* Korneyev (Tachiniscinae) (Korneyev 2012; Korneyev & Norrbom 2006).

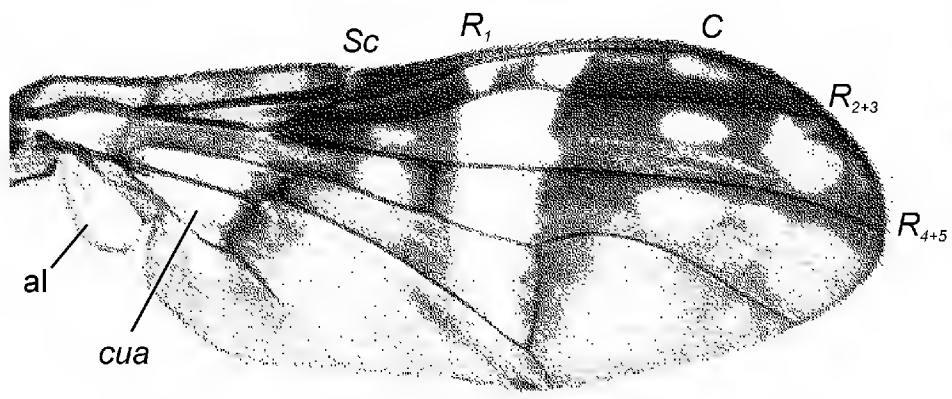
Analyses of molecular data have not yet confirmed relationships among Pyrgotidae, Tachiniscinae and the other Tephritidae *sensu stricto* (except Tachiniscinae). Han & Ro (2009, fig. 3) suggested the sister-group position of Pyrgotidae to Tephritidae *sensu lato* (Tachiniscinae + Tephritidae *sensu stricto*), from a consensus tree derived from Bayesian analysis of the combined sequences of 12S rRNA, 16S rRNA and COII genes, using the GTR + I + G evolutionary model for two Pyrgotidae, two Tachiniscinae and over 60 Tephritidae species. Wiegmann *et al*. (2011, fig. S1), on the contrary, considered Tephritidae (*sensu stricto*) to be sister-group to Tachiniscinae + Pyrgotidae, based on 12 nuclear protein coding genes, 18S and 28S ribosomal DNA and complete mitochondrial genomes by the



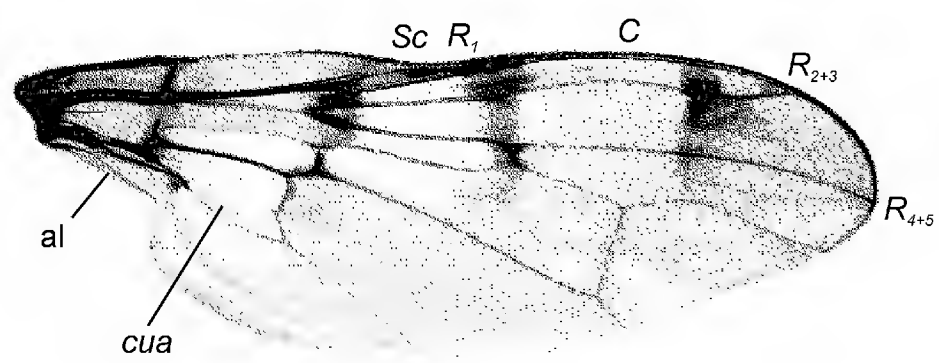
44 *Tephritopyrgota*



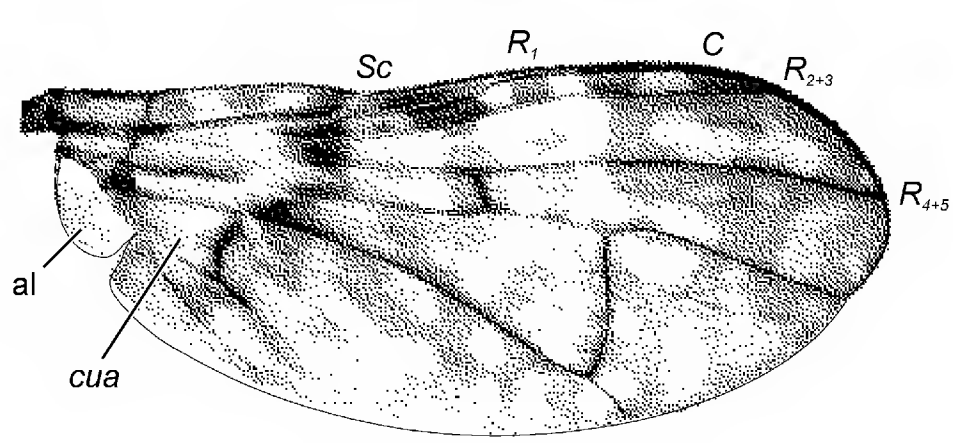
45 *Tephritopyrgota*



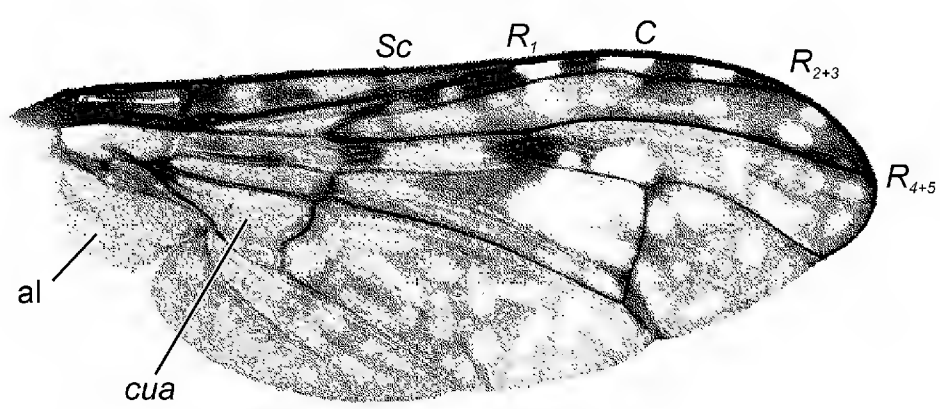
46 *Tephritopyrgota*



47 *Tephritopyrgota*



48 *Tephritopyrgota*



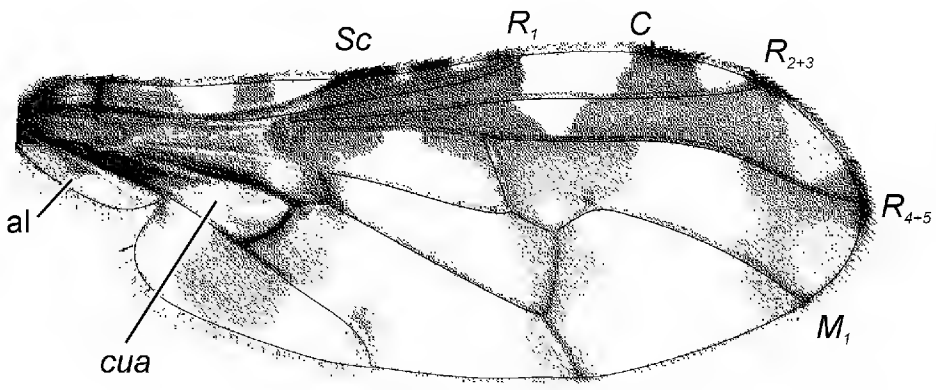
49 *Pyrgotina*

Figs 72.44–49. Wings of Pyrgotidae (dorsal views): (44) *Tephritopyrgota* sp.; (45) *Te. clemelis* Séguy; (46) *Te. spinosa* Hennig; (47) *Te. binodosa* Hennig; (48) *Te. tenuis* Hennig; (49) *Pyrgotina* sp.

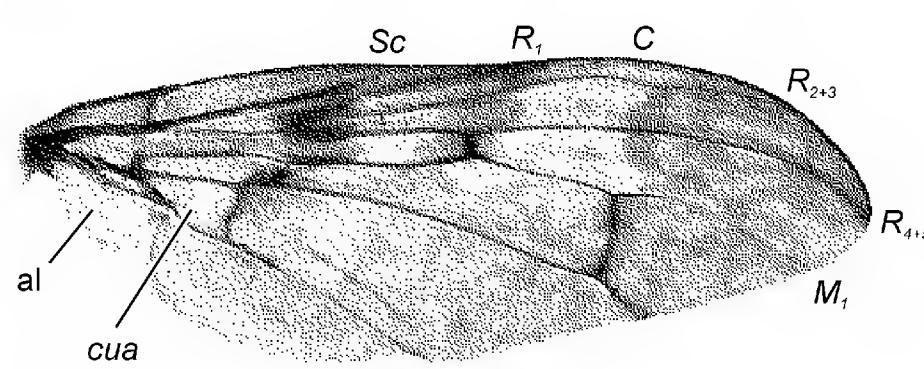
Abbreviations: al – alula; C – costal vein; *cua* – anterior cubital cell; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *Sc* – subcostal vein.

Bayesian analysis as described in that paper, but only four species in the in-group of Tephritidae + Tachiniscinae + Pyrgotidae were analysed. Further studies by Han & Ro (2016) support only the monophyly of Tephritidae (*sensu stricto*) + Tachiniscinae + Ctenostylidae + Pyrgotidae. Adding more taxa and genes in future analyses may resolve this problem.

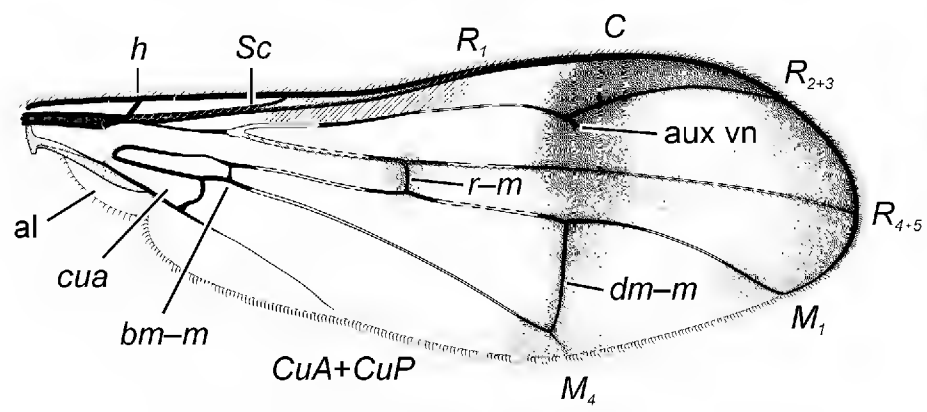
Two subfamilies, Teretrurinae and Pyrgotinae, are currently recognised (McAlpine 1979), but a few archaic South American and Australian monotypic genera apparently deserve additional subfamilies (Korneyev, in prep.). All Afrotropical genera belong to the Pyrgotinae, which can be distinguished by fused abdominal sternites 1 and 2. Within the Pyrgotinae, four tribes



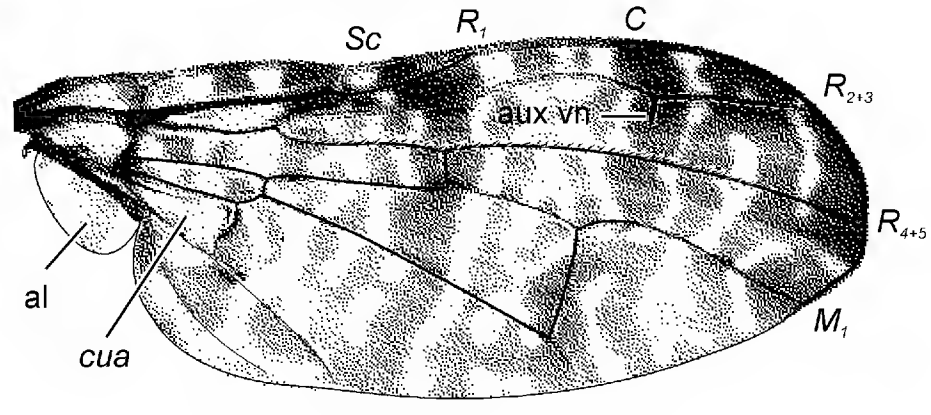
50 *Toxopyrgota*



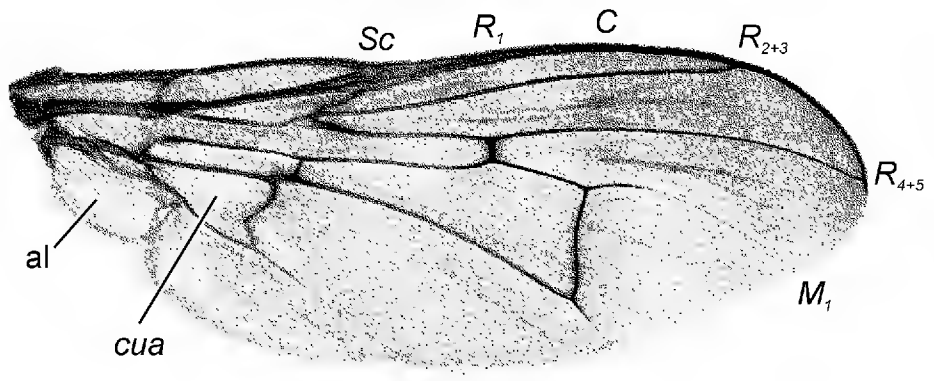
51 *Rhagostira*



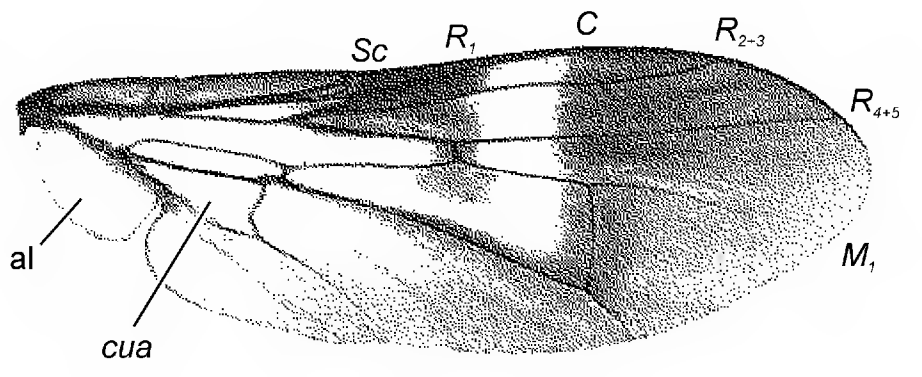
52 *Pyrgotomyia*



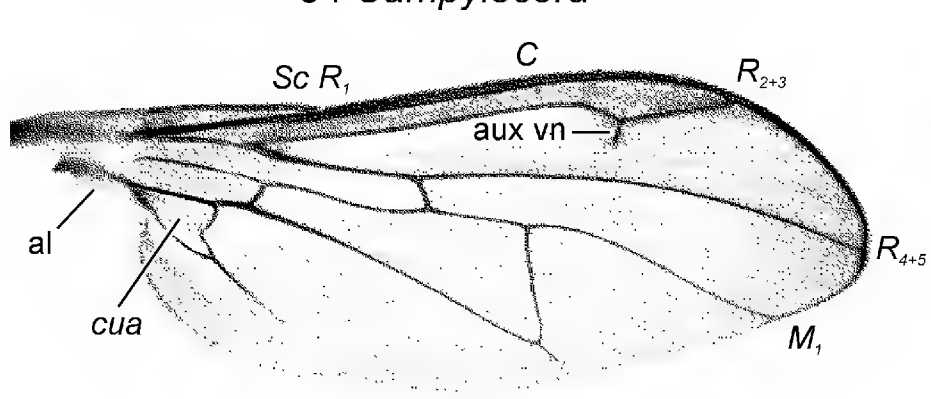
53 *Geloemyia*



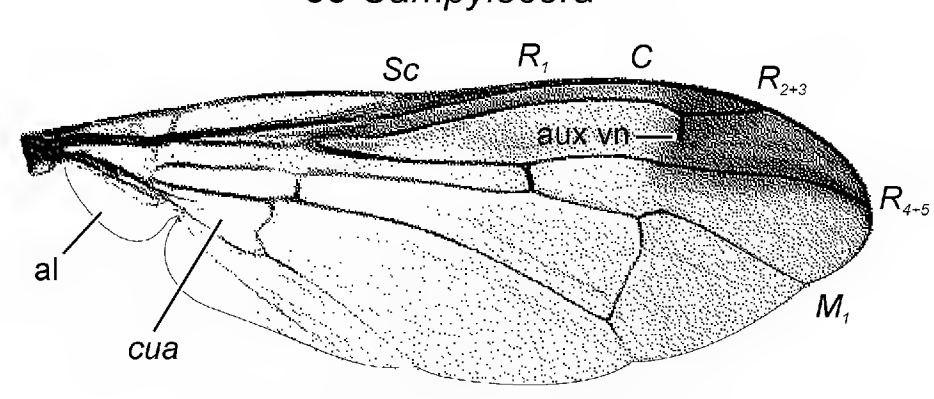
54 *Campylocera*



55 *Campylocera*



56 *Eupyrgota* (*Taeniomastix*)



57 *Eupyrgota* (*Eupyrgota*)

Figs 72.50–57. Wings of Pyrgotidae (dorsal views): (50) *Toxopyrgota inclinata* Hendel; (51) *Rhagostira erlangeri* (Walker); (52) *Pyrgotomyia stuckenbergi* Korneyev; (53) *Geloemyia namibiensis* Korneyev; (54) *Campylocera ferruginea* (Macquart); (55) *C. variceps* (Curran); (56) *Eupyrgota* (*Taeniomastix*) *saegeri* (Vanschuytbroeck); (57) *E.* (*E.*) *caffra* (Hendel).

Abbreviations: al – alula; aux vn – auxiliary vein; *bm–m* – basal medial crossvein; *C* – costal vein; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *dm–m* – discal medial crossvein; *h* – humeral crossvein; M_1 – first branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Sc* – subcostal vein.

are recognised: monotypic Prodalmanniini (Australasian); Toxopyrgotini (Afrotropical); Toxurini (Australasian); and Pyrgotini (sub-cosmopolitan, with subtribes Pyrgotina and Adapsiliina; the last named palaeotropical, with a few genera in the Palaearctic and Australasian Regions). The subtribe Pyrgotina is possibly a paraphyletic group, with Adapsiliina, a derived group nested within it (Korneyev 2016*a*, *b*).

Identification

Pyrgotidae occur in all major zoogeographical regions of the world, predominantly in the tropics. Of the 340 species known globally, 150 are currently known from the Afrotropical Region. Numerous additional undescribed Afrotropical species have been identified in collections and many nominal species are yet to be synonymised (Korneyev unpubl.). Steyskal (1980) recorded 24 genera from the Afrotropical Region. In a series of recent taxonomic revisions (Korneyev 2006*a*, *b*, 2012, 2014*a*, *b*, 2015*a*, *b*, 2016*a*, *b* and in prep.), a number of generic names were found to be synonyms. Here, only 13 genera are considered to occur in the Afrotropics and synonyms are listed in the "Synopsis of the fauna" section below. Pyrgotidae are best direct-pinned in the field (see Chapter 2) for later study.

Key to genera of Afrotropical Pyrgotidae

1. Wing cell *cua* closed by straight or arcuate vein (Fig. 50); frons of head with 2–4 long frontal setae (Fig. 13); depth of gena greater than height of eye (Fig. 13); male hind coxa and trochanter enlarged with projection (Fig. 37); female coxae without clutches of stiff setae; smaller species (body length: 3–4.5 mm). . . . . *Toxopyrgota* Hendel

– Wing cell *cua* closed by angulate vein, forming triangular posteroapical lobe (e.g., Figs 44–49, 51–57); frons of head without frontal setae; gena at most as high as eye (e.g., Figs 2–12); male hind coxa and trochanter unmodified; female coxae sometimes with clutches of stiff setae (e.g., Fig. 43); larger species (body length: 3.5–18 mm, usually 4.5–13 mm) 2

2. Antennal postpedicel extremely long, > 1.2 × as long as eye height (Fig. 6); thorax without anterior notopleural, proepisternal, supra-alar, dorsocentral, acrostichal and basal scutellar setae . . . . . *Hendelpyrgota* Vanschuytbroeck

– Antennal postpedicel shorter than eye height (e.g., Figs 3–5); thorax with anterior notopleural, proepisternal, supra-alar, dorsocentral and usually acrostichal and basal scutellar setae (e.g., Figs 26, 28). 3

3. Costal wing vein (*C*) reaching vein M_1 (e.g., Figs 56, 57) 4

– Costal wing vein (*C*) not reaching vein M_1, or at least strongly thinned after apex of vein R_{4+5} or entirely reduced (e.g., Figs 51, 54, 55) 12

4. Wing vein R_{4+5} setulose dorsally (e.g., Figs 52, 53); mesonotum of thorax with 3–4 dorsocentral setae (usually 1 presutural) (e.g., Figs 26, 27). 5

– Wing vein R_{4+5} bare (e.g., Figs 44–49); mesonotum of thorax with 2 (1) dorsocentral setae (e.g., Figs 28, 29). 6

5. Antennal pedicel and scape elongate, each at least 2 × as long as wide (Fig. 8) . . . . .*Pyrgotomyia* Hendel

– Antennal pedicel and scape short, as long as wide, or at most 1.5 × longer than wide (Fig. 5) . . . . . *Geloemyia* Hendel

6. Head with epistoma high, at least 0.7 × as high as antennal groove (e.g., Figs 15, 16), in dubious cases (e.g., Figs 17, 18), wing with reticulate or banded pattern, including hyaline maculae; head with facial carina separating antennal grooves (e.g., Figs 15–18); vein R_{2+3} usually without auxiliary vein (e.g., Figs 44–49); oviscape of female with unpaired medial apicoventral hook 7

– Head with epistoma low, at most 0.5 × as high as antennal groove (e.g., Figs 20–22); head with facial carina (e.g., Figs 20, 21) inconspicuous (e.g., Fig. 22) or absent (as in Figs 23–25); wing usually with auxiliary vein on vein R_{2+3} (e.g., Figs 56, 57), entirely hyaline, or with darker apical ⅓ or widely brown, but not reticulate; oviscape of female either with paired sclerotised apicoventral hooks (ovipositungi) (e.g., Figs 73, 74) or without hooks. 8

7. Ocellar, vertical and orbital setae on head (Fig. 7) and postpronotal, presutural supra-alar and usually dorsocentral setae on thorax (Fig. 29) absent; head (Fig. 18) with frons narrow, 3 × as long as wide; medioventral hook on female oviscape wide, clearly microtrichose anteroventrally . . . . . *Pyrgotina* Malloch

– Most or all of above noted setae, well-developed (Figs 11, 12); head (Figs 16, 17) with frons at most 2 × as wide as long; medioventral hook on female oviscape bare. . . . . .*Tephritopyrgota* Hendel

8. Femora with 2 rows of short, thickened setulae apicoventrally (e.g., Figs 39, 40). 9

– Femora with thin, long setulae or bare apicoventrally (e.g., Fig. 38) 10

9. Prosternum of thorax with pair of nipple-like projections ventrally (Fig. 30); female oviscape with paired apicoventral hooks (ovipositungi) (Fig. 74) . . . . . *Eupyrgota* Hendel

– Prosternum of thorax with pair of low, slightly projected ridges anteroventrally (as in Fig. 31); female oviscape without hooks . . . . . *Afropyrgota* Korneyev

10. Upper calypter of wing with stout black cilia (Fig. 36); vein R_{2+3} with auxiliary vein (Fig. 33); gena with large sclerotised subocular sclerite (Fig. 10); large species (wing length: 7–18 mm), with long thin legs and first abdominal segment (Fig. 33). . . . . *Siridapha* Enderlein

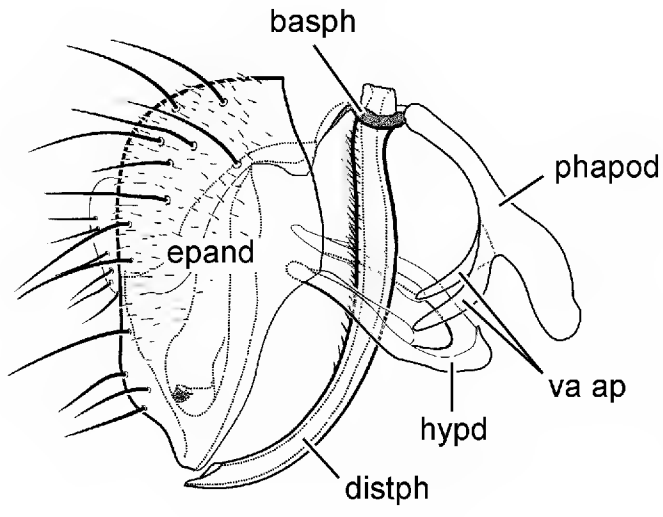
– Upper calypter of wing with fine cilia; vein R_{2+3} without auxiliary vein; other characters variable . . . 11

11. Antenna long, pedicel 1.5–2 × as long as wide at apex; gena usually with large sclerotised subocular dilation; female often with mid femoral organ bare; male usually with long setae on sternite 3; larger species (wing length: 7–13 mm). . . . . *Adapsilia* Waga

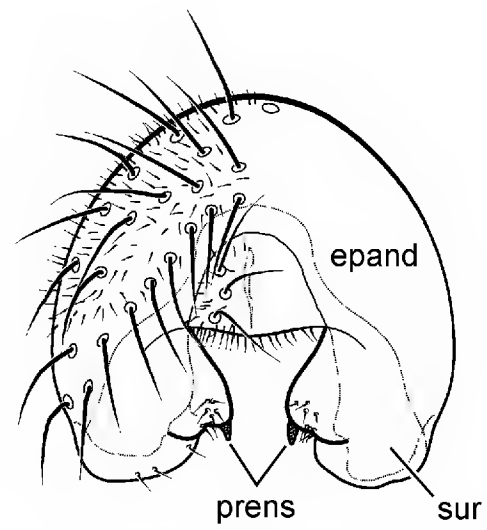
– Antenna short, pedicel as long as wide at apex; gena soft, without subocular sclerite (as in Figs 9, 12); female invariably without femoral organ; male without long, dense setae on sternites; smaller species (wing length: 4–6.5 mm) . . . . . Undescribed genus

12. Wing membrane grey, with reticulate or mottled pattern formed by hyaline maculae (Fig. 51); head with epistoma high, usually as high as antennal groove (as in Figs 16, 18), rarely low (Fig. 19); gena soft, without subocular sclerite (Fig. 9). . . . . *Rhagostira* Enderlein

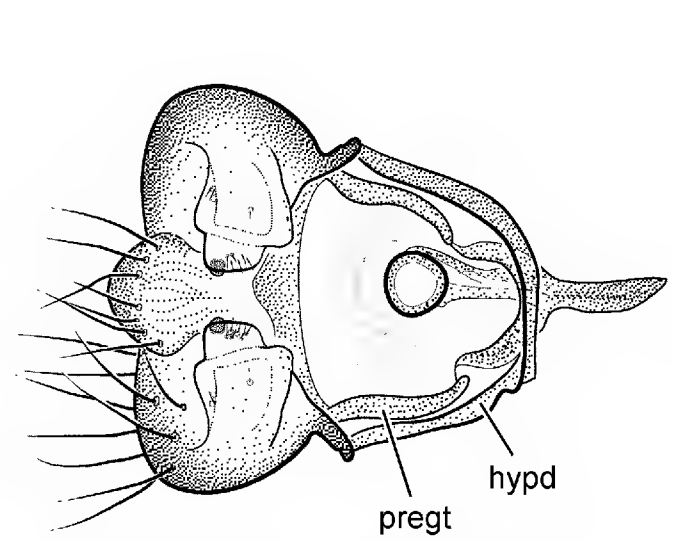
– Wing membrane uniformly hyaline, grey or brown, sometimes with darkened apex or crossveins (Figs 54, 55), but not reticulate; head with epistoma very low (Fig. 20); gena with clearly expressed, usually large subocular sclerite (Fig. 2) . . . . . *Campylocera* Macquart



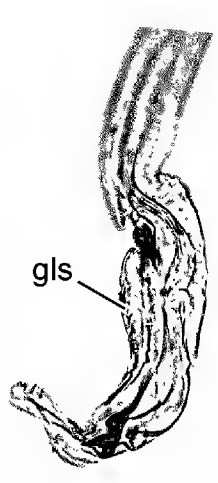
58 *Toxopyrgota* ♂



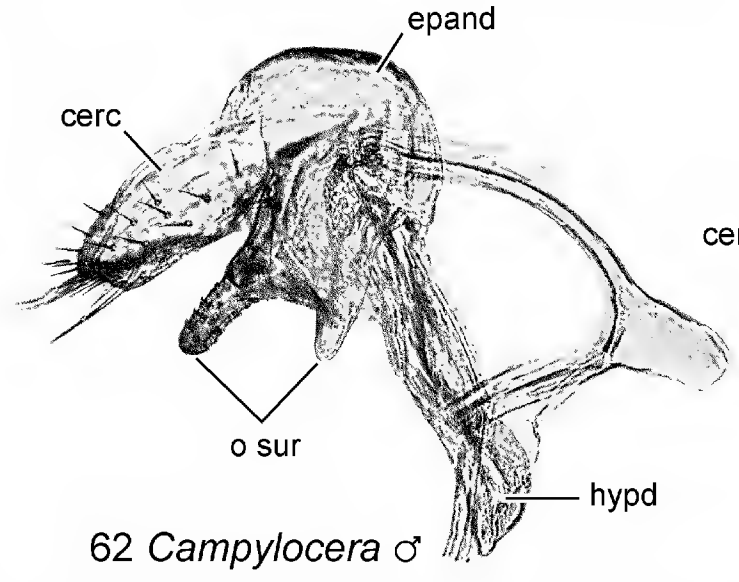
59 *Toxopyrgota* ♂



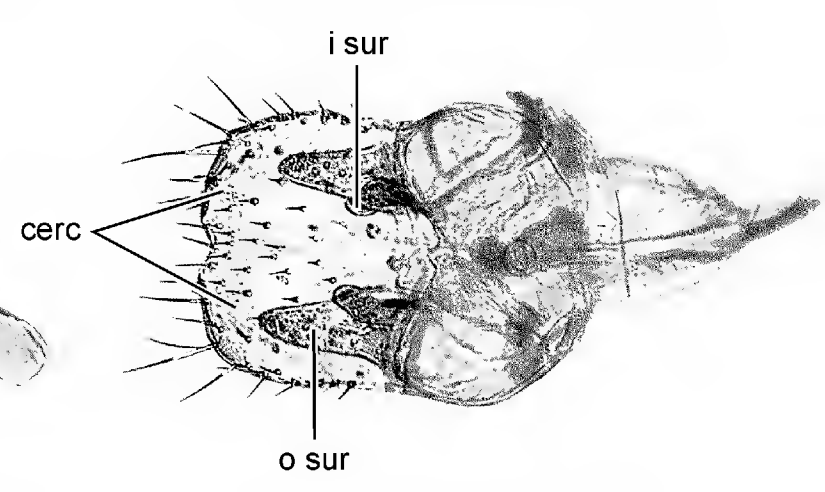
60 *Toxopyrgota* ♂



61 *Toxopyrgota* ♂



62 *Campylocera* ♂



63 *Campylocera* ♂

Figs 72.58–63. Male terminalia of Pyrgotidae: (58) epandrium and hypandrium of *Toxopyrgota inclinata* Hendel, lateral view; (59) same, epandrium, posterior view; (60) same, epandrium and hypandrium, ventral view; (61) same, apex of distiphallus lateral view; (62) epandrium and hypandrium of *Campylocera ferruginea* (Macquart), lateral view; (63) same, ventral view.

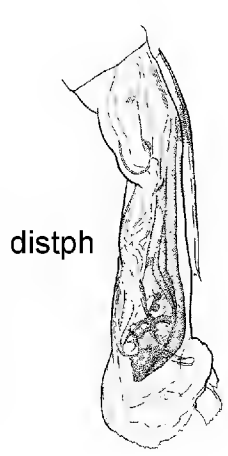
Abbreviations: basph – basiphallus; cerc – cercus; distph – distiphallus; epand – epandrium; gls – glans; hypd – hypandrium; i sur – inner surstylus; o sur – outer surstylus; phapod – phallapodeme; pregt – pregonite; prens – prensisetae; sur – surstylus; va ap – vanes of apodeme.

Synopsis of the fauna

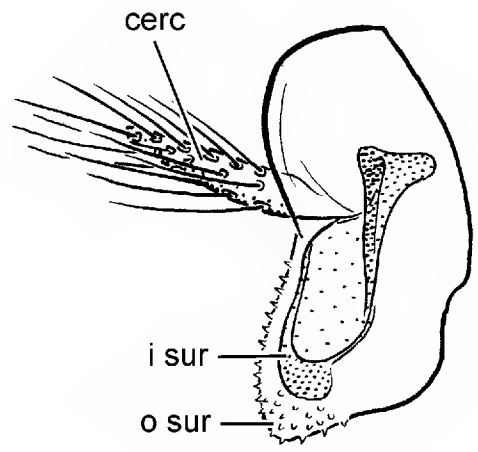
***Adapsilia* Waga** (Pyrgotinae: Pyrgotini: Adapsiliina)**.** A genus of three to seven species occurring in the Oriental and Palaearctic Regions. Some species are undescribed or require synonymy. The diagnosis and concept of the genus need reconsideration and most species currently assigned to it belong to other genera (Korneyev 2014*a*, unpubl.). No continental Afrotropical species are known, but a single specimen of an undescribed species is known from Madagascar (Korneyev, in prep.). The biology and immature stages remain unknown.

***Afropyrgota* Korneyev** (Pyrgotinae: Pyrgotini: Adapsiliina)**.** An endemic genus with five species occurring from Nigeria to Kenya and Tanzania and differing from superficially similar *Eupyrgota* by the saddle-like prosternum without nipple- or finger-like projections ventrally (as in Fig. 31) and the female ovi-scape does not bear posterolaterally directed sclerotised hooks (Korneyev 2015*a*). The biology and immature stages remain unknown. An identification key to species was provided by Korneyev (2015*a*).

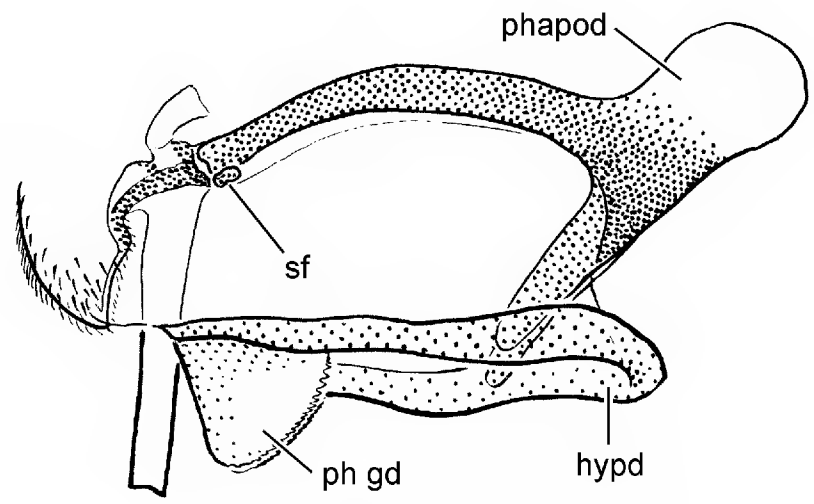
***Campylocera* Macquart** (Pyrgotinae: Pyrgotini: Adapsiliina)**.** A genus of *ca* 50 nominal species, described mainly from the continental Afrotropical Region, with about five species known from Australasia (Papuan sub-region and Northern Australia) and the Oriental Region. The genus can be distinguished by the incomplete costal vein (*C*) terminating at vein R_{4+5} (Figs 54, 55); the low epistoma (Fig. 20); the subocular sclerite well-expressed (Fig. 2), but reduced in species with very low gena (Fig. 3); the mid femur invariably without a femoral organ and the male terminalia with the cercus flattened dorsoventrally, this large, slightly longer and wider than epandrium (Figs 62, 63) (Korneyev 2016*b*). Descriptions of species are largely based on external characters and detailed studies of the terminalia need to be conducted. Many nominal species can only be distinguished from females or (rarely) from males alone and due



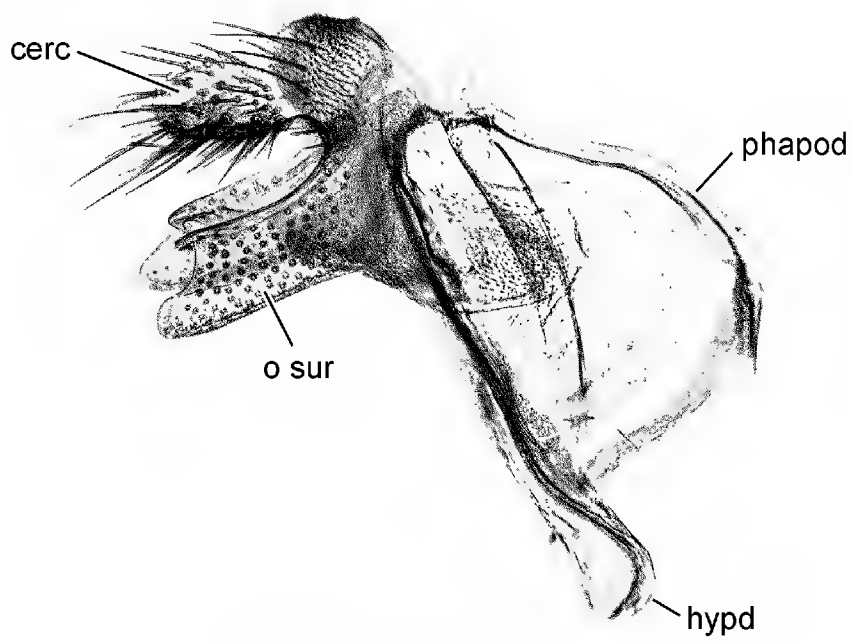
64 *Adapsilia* ♂



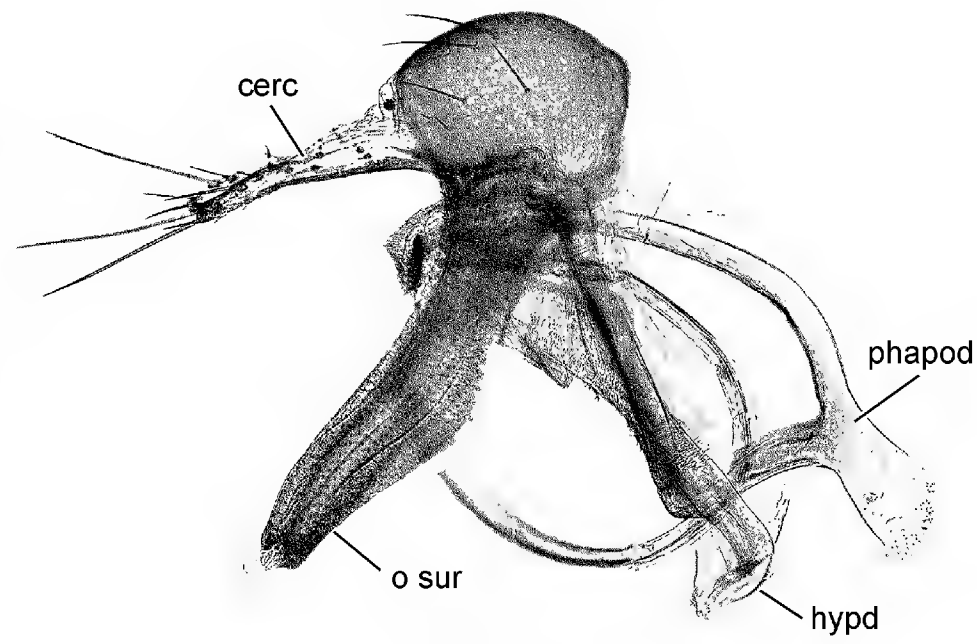
65 *Eupyrgota* (*Eupyrgota*) ♂



66 *Eupyrgota* (*Eupyrgota*) ♂



67 *Geloemyia* ♂



68 *Siridapha* ♂

Figs 72.64–68. Male terminalia of Pyrgotidae: (64) apex of distiphallus of *Adapsilia coarctata* (Waga), lateral view (non-Afrotropical); (65) epandrium of *Eupyrgota* (*Eupyrgota*) *wagai* (Bigot), lateral view (non-Afrotropical); (66) same, hypandrium and base of phallus, lateral view; (67) epandrium and hypandrium of *Geloemyia namibiensis* (Hennig), lateral view; (68) same, *Siridapha mulguensis* (Vanschuytbroeck).

Abbreviations: cerc – cercus; gls – glans; hypd – hypandrium; i sur – inner surstylus; o sur – outer surstylus; ph gd – phallic guide; phapod – phallapodeme; sf – sensillar field.

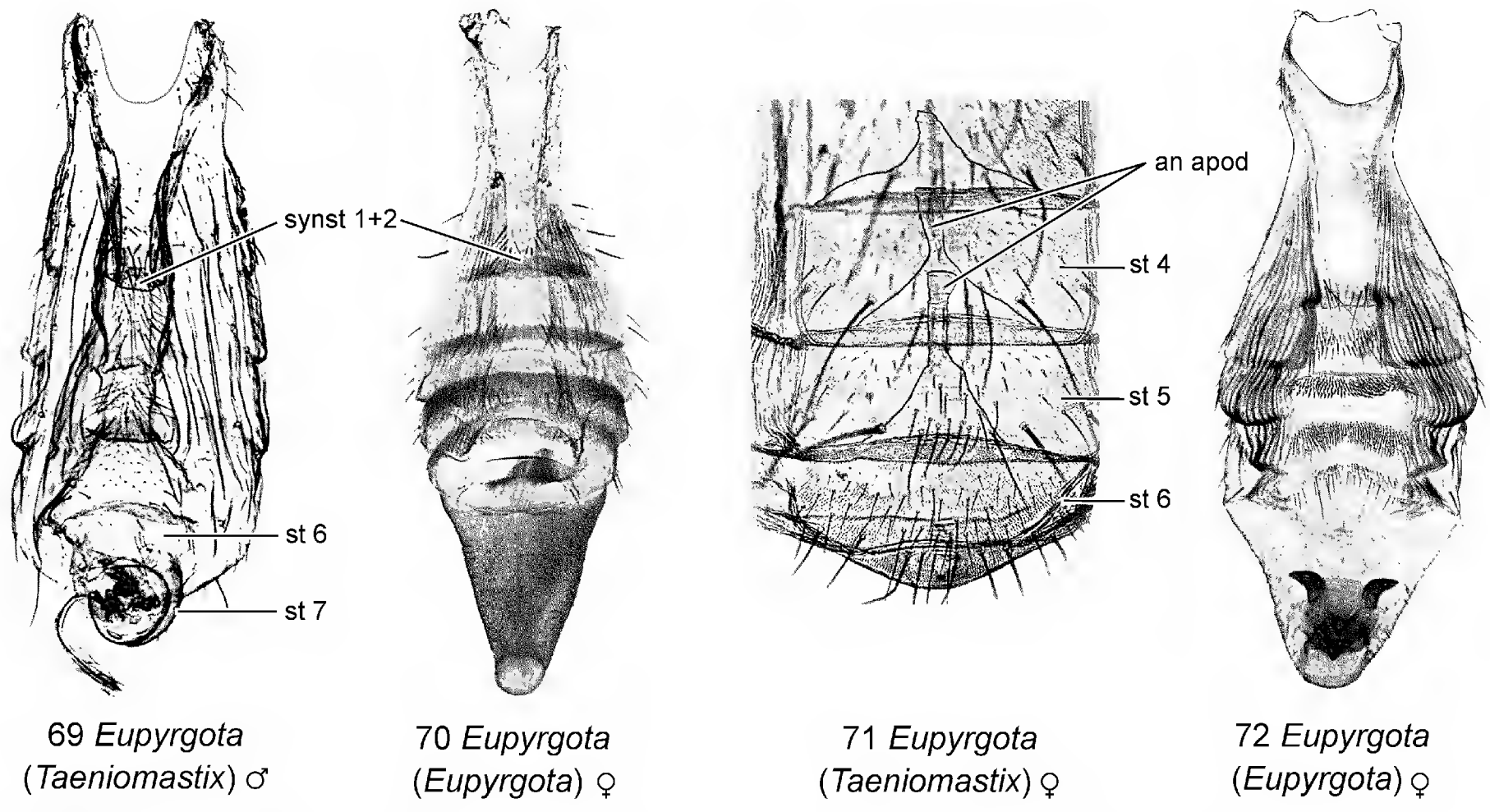
to sexual dimorphism in head shape and wing pattern, sexes cannot be reliably associated in many cases. Generic synonyms include: *Clemaxia* Enderlein, *Congopyrgota* Aczél, *Diasteneura* Hendel, *Dicrostira* Enderlein, *Hexamerinx* Enderlein, *Hypotyphla* Hendel, *Hypotyphlina* Enderlein, *Lygiohypotyphla* Enderlein and *Prohypotyphla* Hendel (Korneyev 2016*b*). The biology and immature stages of Afrotropical species remain unknown. No comprehensive identification key to species has been published and the genus requires thorough taxonomic revision.

***Eupyrgota* Coquillett** (Pyrgotinae: Pyrgotini: Adapsiliina)**.** A genus of 38 described species occurring in the Afrotropical, Australasian, Oriental and Palaearctic Regions (Fig. 32). Two of the three recognised subgenera occur in the Afrotropical Region and Old World species lacking a facial carina and formerly assigned to *Apyrgota* Hendel mostly belong here. The subgenus *Eupyrgota sensu stricto* (including *Apyrgota* and *Peltodasia* Enderlein), comprises nine species known throughout the Afrotropical Region (Korneyev 2006*a*, *b*; 2014*a*) and 15 in the Oriental Region and adjoining parts of the Palaearctic and Australasian Regions (Korneyev 2014*a*). The subgenus *E.* (*Taeniomastix* Enderlein) corresponds to the *spinifemur*-group (*sensu* Korneyev 2006*a*). Two species, *E.* (*T.*) *saegeri* (Vanschuytbroek, 1963) and *E.* (*T.*) *spinifemur* (Hendel, 1934) have been recorded from the Afrotropics (Korneyev 2006*a*) and four species from the Oriental and Palaearctic Regions; some undescribed species recognised in collections occur in the Papuan sub-region (Korneyev 2014*b*). The biology and immature stages of only one Afrotropical species are known (see above). Identification keys to species are provided by Korneyev (2006*b*; 2014*a*, *b*).

***Geloemyia* Hendel** (Pyrgotinae: Pyrgotini: Adapsiliina)**.** A genus of nine described species, occurring in the Afrotropical and Oriental Regions and adjoining parts of the Palaearctic Region (Korneyev 2015*b*). One species, *G. namibica* Korneyev 2015, is recorded from Namibia and another, *G. trifasciata* (Enderlein, 1942), from Madagascar. Generic synonyms include: *Dicranostira* Enderlein, *Parageloemyia* Hendel and *Trichempodia* Malloch (Korneyev 2015*b*). One Palaearctic species was reared from adult *Serica* MacLeay (Scarabaeidae: Melolonthinae: Sericini) (Nartshuk & Korneyev 2005), but the biology and immature stages otherwise remain unknown. Afrotropical species can be identified using the identification key provided by Korneyev (2015*b*).

***Hendelpyrgota* Vanschuytbroeck** (Pyrgotinae: Pyrgotini: Adapsiliina)**.** An endemic monotypic genus, with the single species, *H. longicornis* Vanschuytbroeck, 1963, recorded from Democratic Republic of Congo, Malawi and Tanzania. The species has an elongate body, large wings, very long antenna (Fig. 6) and a high face without a carina (Fig. 24). Males have not been recognised in collections. The biology and immature stages remain unknown.

***Pyrgotina* Malloch** (Pyrgotinae: Pyrgotini: Pyrgotina)**.** An endemic genus of seven described species, with six to eight additional species recognised in collections (Korneyev, unpubl.). Generic synonyms include *Trichellopsis* Bezzi (Steyskal 1980) and likely also *Platynostira* Enderlein. The biology and immature stages remain unknown and no comprehensive identification key is currently available.



Figs 72.69–72. Male and female abdomens and terminalia of Pyrgotidae, ventral views: (69) male abdomen of *Eupyrgota* (*Taeniomastix*) *saegeri* (Vanschuytbroeck); (70) female abdomen of *E.* (*E.*) *vespiformis* (Enderlein); (71) female abdominal sternites of *E.* (*T.*) *saegeri*; (72) female abdomen and terminalia of *E.* (*E.*) *echinata* Korneyev.

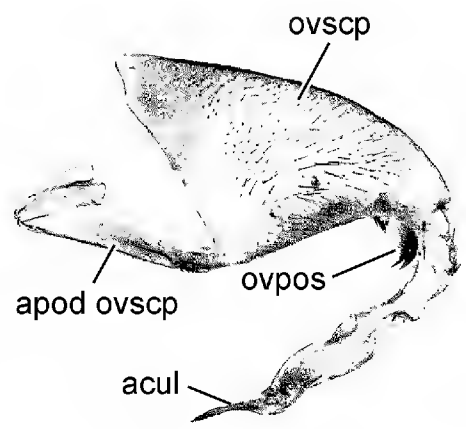
Abbreviations: an apod – anteromedial apodeme of sternite; st – sternite; synst – synsternite.

***Pyrgotomyia* Hendel** (Pyrgotinae: Pyrgotini: Adapsiliina)**.** An endemic genus, with six nominal species recorded from the continental Afrotropical Region. One species, described from a male, cannot be associated with others described from females. Generic synonymy includes *Metropina* Enderlein (Korneyev 2012). The biology and immature stages remain unknown. Korneyev (2012) revised the genus and provided an identification key to known species.

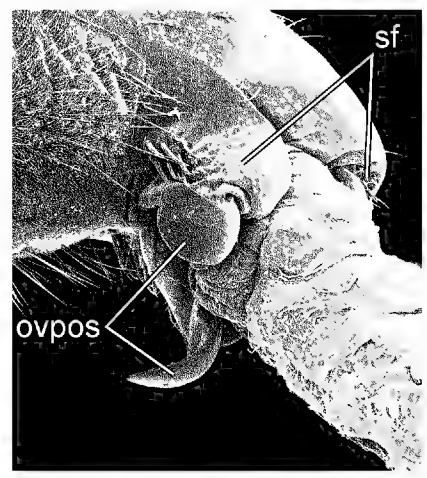
***Rhagostira* Enderlein** (Pyrgotinae: Pyrgotini: Pyrgotina)**.** An endemic genus of nine nominal species occurring in the continental Afrotropics. The genus is related to *Tephritopyrgota*, differing mainly in the costal vein (C) terminating at vein R_{4+5} (Fig. 51). Detailed studies of *Tephritocampylocera carbonaria* Hendel, 1914 have indicated that it possesses an entirely developed costal vein reaching vein M_1 (although Hendel (1914) insisted it to be incomplete) and belongs in the genus *Tephritopyrgota* (Korneyev, in prep.). Redefinition of the generic concept of *Rhagostira* will likely require inclusion of *Tephritocampylocera auctt. pro parte major* and *Tephritohypotyphla* Vanschuytbroeck. The biology and immature stages remain unknown and no identification key is currently available.

***Siridapha* Enderlein** (Pyrgotinae: Pyrgotini: Adapsiliina)**.** An endemic genus of three described and three or four undescribed species, recorded from Bioko Is. (Equatorial Guinea) (as Fernando Póo), Cameroon to Kenya and Tanzania (Korneyev, in prep.) (Fig. 33). The genus includes long, narrow-bodied, long-legged flies, superficially resembling parasitic wasps of the genus *Ophion* F. (Hymenoptera: Ichneumonidae: Ophioninae); the females often with strong setae on the mid and hind coxae and ventral part of the katepisternum and abdominal sternites (Fig. 33). The biology and immature stages remain unknown and no identification key is currently available.

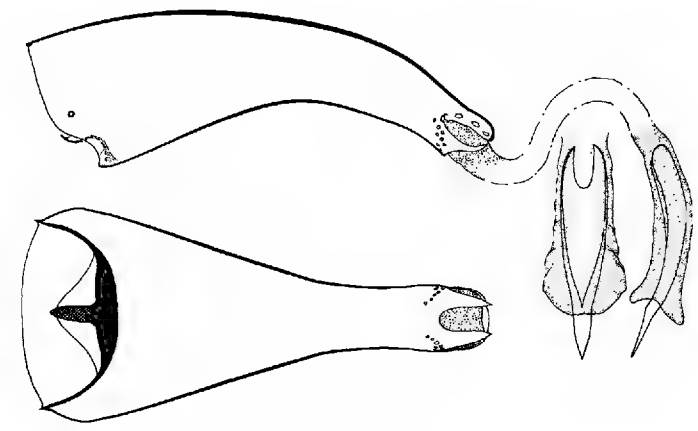
***Tephritopyrgota* Hendel** (Pyrgotinae: Pyrgotini: Pyrgotina)**.** One of the two most common genera of Afrotropical pyrgotids (Fig. 35). Eighteen species are recorded from the continental Afrotropics and 19 are endemic to Madagascar. Three to four species are known from the Oriental Region and adjacent parts



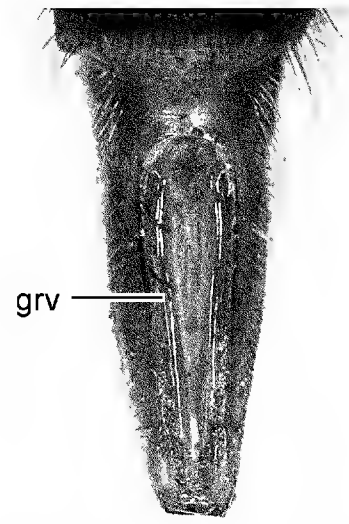
73 *Eupyrgota* (*Eupyrgota*) ♀



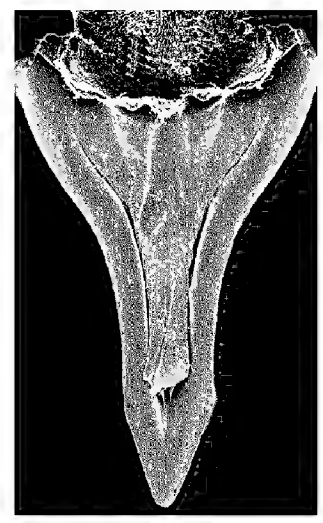
74 *Eupyrgota* (*Eupyrgota*) ♀



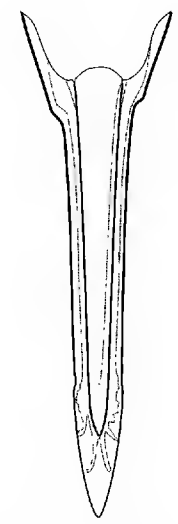
75 *Toxopyrgota* ♀



76 *Siridapha* ♀



77 *Eupyrgota* (*Eupyrgota*) ♀



78 *Pyrgotomyia* ♀

79 *Siridapha* ♀

80 *Campylocera* ♀

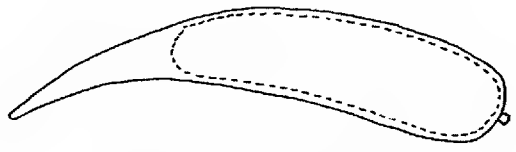
Figs 72.73–80. Female abdomens and terminalia of Pyrgotidae: (73) ovipositor of *Eupyrgota* (*Eupyrgota*) *latipennis* (Walker), lateral view; (74) apex of oviscape of *E.* (*E.*) *caffra* (Hendel), ventral view; (75) ovipositor of *Toxopyrgota inclinata* Hendel, lateral (above) and ventral (below) views; (76) oviscape of *Siridapha filipalpis* Enderlein, ventral view; (77) aculeus of *E.* (*E.*) *caffra*, ventral view; (78) same, *Pyrgotomyia terebrans* Korneyev; (79) same, *S. filipalpis*; (80) same, *Campylocera angustigenis* Hendel. Fig. 75 (after Steyskal 1972, fig. 11).

Abbreviations: acul – aculeus; apod ovscp – apodeme of oviscape; grv – groove; ovpos – ovipositungus; ovscp – oviscape; sf – sensillar field.

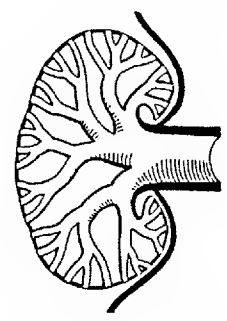
of the Palaearctic. Monophyly of the genus is dubious and its concept needs reconsideration and will likely require inclusion of *Euthioza* Enderlein, *Stypina* Enderlein and *Tephritocampylocera* Hendel. The biology and immature stages remain unknown. Madagascan species were described and keyed by Hennig (1961), but most continental Afrotropical species are still poorly distinguishable and in need of revision.

***Toxopyrgota* Hendel** (Pyrgotinae: Toxopyrgotini)**.** An endemic monotypic genus, with the single described species, *T. inclinata* Hendel, 1914 (Fig. 34), recorded from Ethiopia to Malawi (Korneyev 2016a). The species is relatively small, long-setulose, with well-developed frontal setae (Fig. 13), a reduced (possibly non-functional) proboscis (Fig. 13) and wing cell *cua* closed by an arcuate vein, the cell lacking the posteroapical lobe (Fig. 50). The biology and immature stages of the species remain unknown.

Undescribed genus (Pyrgotinae: Pyrgotini: Adapsiliina)**.** The single species, originally described as *Euthioza nigrocristata* Enderlein, 1942 and recorded from Tanzania to South Africa, actually belongs to an undescribed genus (Korneyev, in prep.). The species can be distinguished using the above identification key. The biology and immature stages remain unknown.

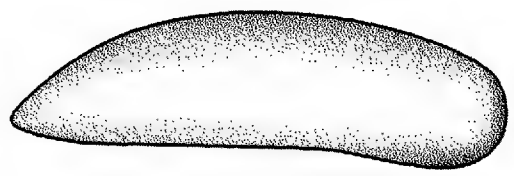


81 *Eupyrgota* (*Asiapyrgota*)

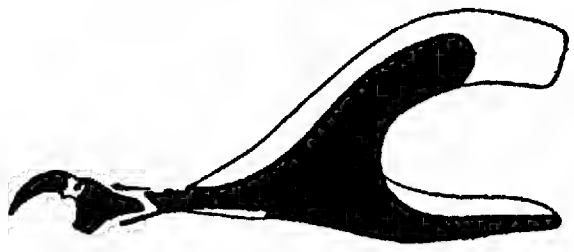


83 *Eupyrgota* (*Asiapyrgota*)

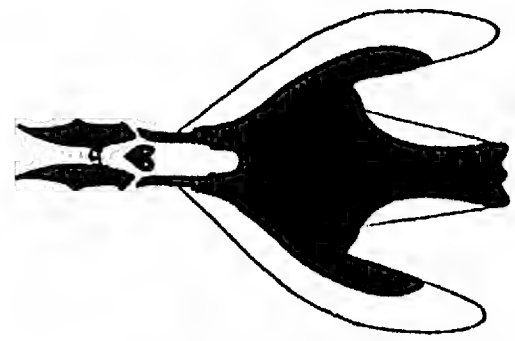
84 *Eupyrgota* (*Asiapyrgota*)



82 *Eupyrgota* (*Eupyrgota*)



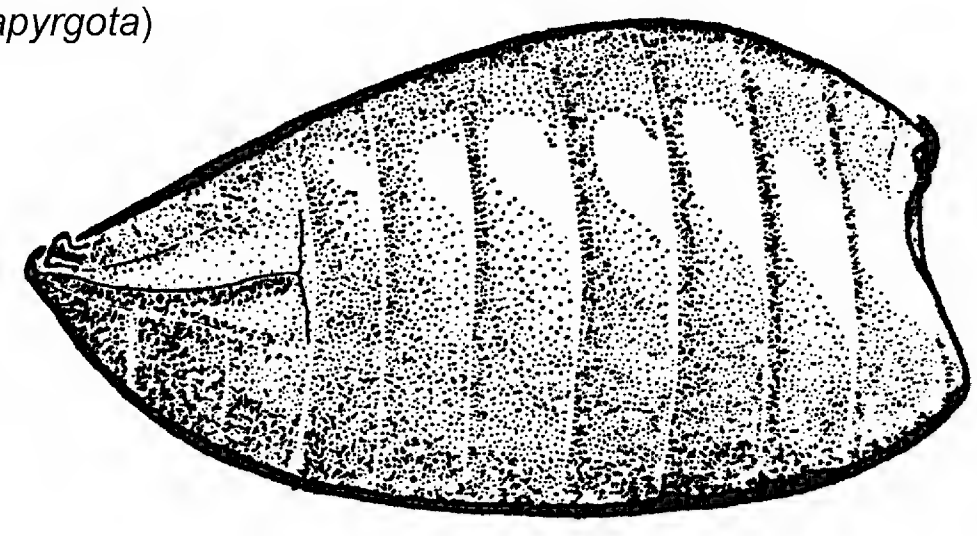
85 *Eupyrgota* (*Asiapyrgota*)



86 *Eupyrgota* (*Asiapyrgota*)

87 *Eupyrgota* (*Eupyrgota*)

88 *Eupyrgota* (*Eupyrgota*)



89 *Eupyrgota* (*Asiapyrgota*)

Figs 72.81–89. Immature stages of Pyrgotidae: (81) egg of *Eupyrgota* (*Asiapyrgota*) *flaviseta* Aldrich, lateral view (non-Afrotropical); (82) same, *E.* (*E.*) *caffra* (Hendel); (83) prothoracic spiracle of *E.* (*A.*) *flaviseta*, lateral view; (84) same, posterior spiracle, caudal view; (85) cephaloskeleton of *E.* (*A.*) *flaviseta*, lateral view; (86) same, ventral view; (87) puparium of *E.* (*E.*) *latipennis* (Walker), in a beetle's abdomen, lateral view; (88) same, posterior view; (89) puparium of *E.* (*A.*) *flaviseta*, lateral view. Figs 81, 83–86, 89 (Clausen *et al*. 1933, figs 10A, B, C, E, 11A).

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CTENOSTYLIDAE 73

(Ctenostylid Flies)

Valery A. Korneyev and David A. Barraclough

Fig. 73.1. Female of *Ramuliseta dolini* Korneyev (Madagascar) (photograph © V. Korneyev).

Diagnosis

Medium- to large-sized (body length: 3.5–13.0 mm) nocturnal, long-legged acalyptrate flies with patterned wings (Fig. 1).

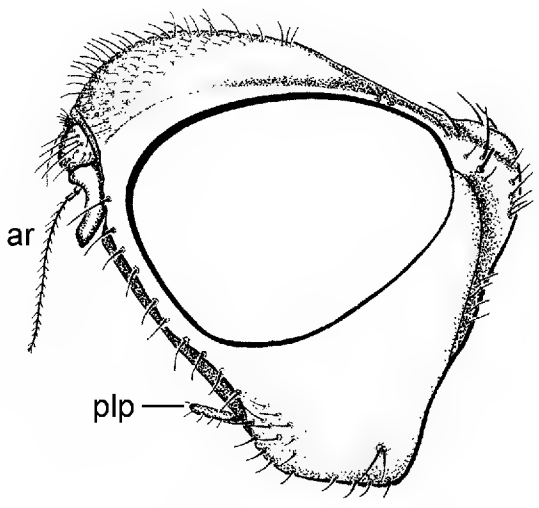
Head large, almost as bulky as thorax (Fig. 5), sexually dimorphic: male arista simple, short plumose (Figs 2, 3); female arista strongly dendritically branched (Figs 4, 5); frons usually narrower in males (Fig. 3) and wider in females (Fig. 4); ocelli lacking; proboscis rudimentary or absent, whereas palpi present in Afrotropical species (Figs 2–4).

Thorax (Fig. 5) short, with transverse prosternum; notopleuron large, bearing 1 seta and 2–3 setulae; anepisternum short; anepimeron setulose; anatergite large and swollen; thoracic spiracles circular, bare. Wing (Figs 6–8) with only subcostal break of costal vein (*C*); subcostal vein (*Sc*) evanescent in apical ⅓; vein R_1 setulose dorsally; cell *bm* open anterobasally; cell *cua* without posteroapical prolongation (lobe); vein A_1 usually distinct distal to alula, at least as a fold. Legs without setae, only with short setulae (Fig. 5); mid tibia without apicoventral spur; hind tibia constricted subbasally.

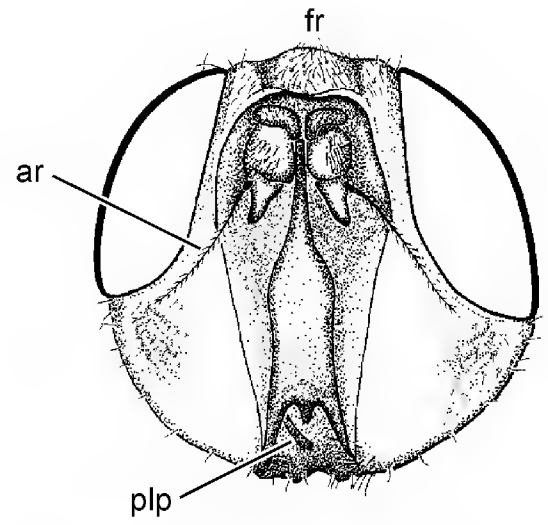
Abdomen with syntergite 1 + 2 more or less petiolate (Fig. 1); sternites 1 and 2 at least partially fused; male with 5 abdominal spiracles; in Afrotropical species segments 6 and 7 inconspicuous or absent; sternite 8 large, setulose (Fig. 12); male terminalia with strongly reduced hypandrium and vanes of phallapodeme

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2021. Manual of Afrotropical Diptera. Volume 3. Brachycera—Cyclorrhapha, excluding Calyptratae. *Suricata* 8. South African National Biodiversity Institute, Pretoria; pp. 1753–1756.

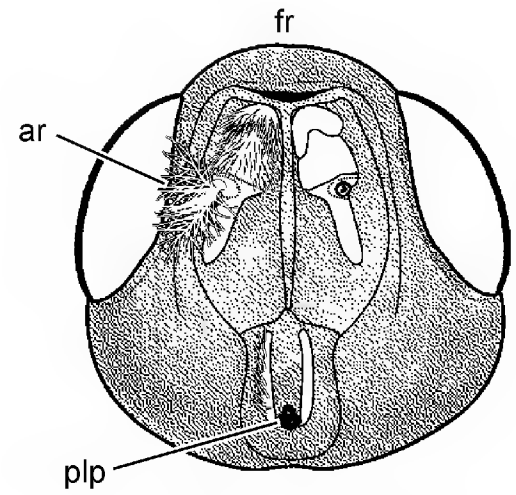
(Fig. 10); epandrium setulose, with short surstylus, subepandrial segment short setulose, without prensisetae (Fig. 10); phallus simple, long (Figs 11, 12) and coiled in a pocket in right dorsal side of abdomen, in *Ramuliseta* Keiser without membranous glans; ejaculatory apodeme large, fan-like, as in Tephritidae and Pyrgotidae (Fig. 9); females, as in other Tephritoidea, with telescopic ovipositor (Fig. 13), including sclerotised oviscape, or tergosternum 7, consisting of narrow tergite and large, setulose and convex sternite (Fig. 13); eversible membrane (Fig. 13) finely microtrichose, without taeniae; aculeus reduced to non-sclerotised tube (tergosternite 8), with fused, short and blunt cerci dorsoapically (Figs 13, 14); no spermathecae detected; vagina in Neotropical *Furciseta* Aczél full of first-instar larvae or eggs with larvae, *i.e.*, flies are viviparous or ovoviviparous.



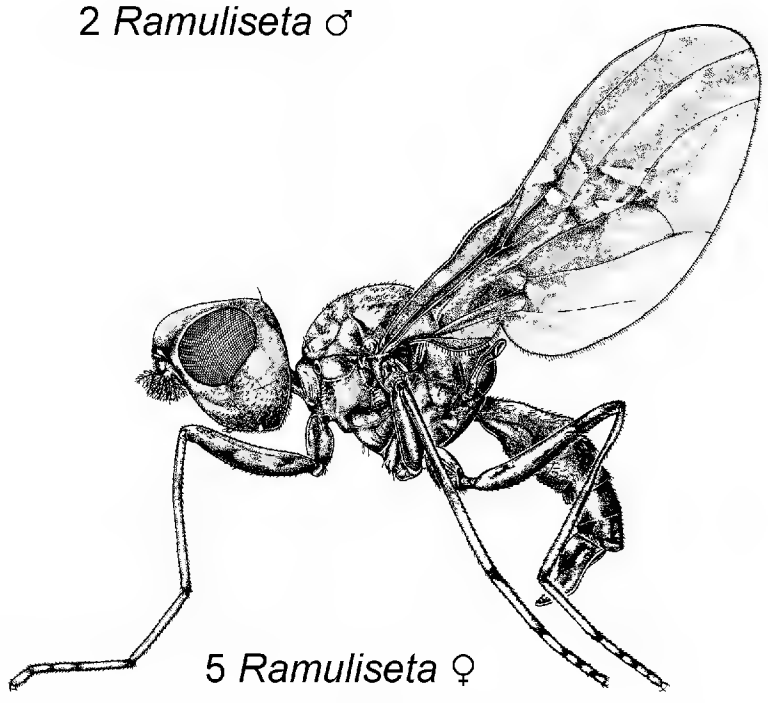
2 *Ramuliseta* ♂



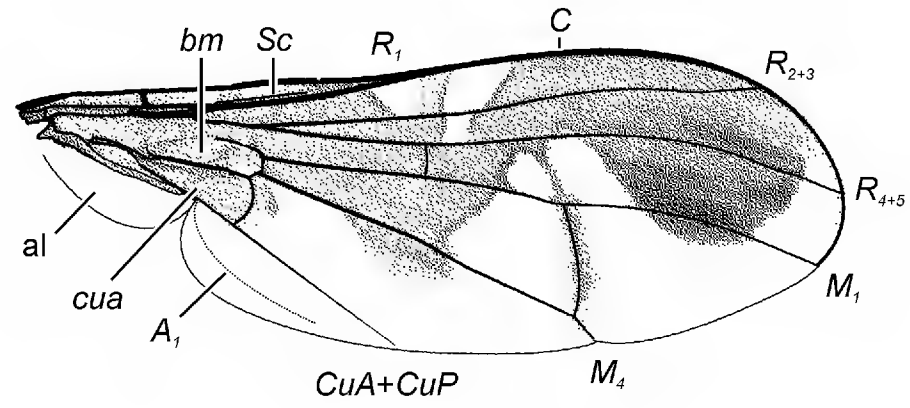
3 *Ramuliseta* ♂



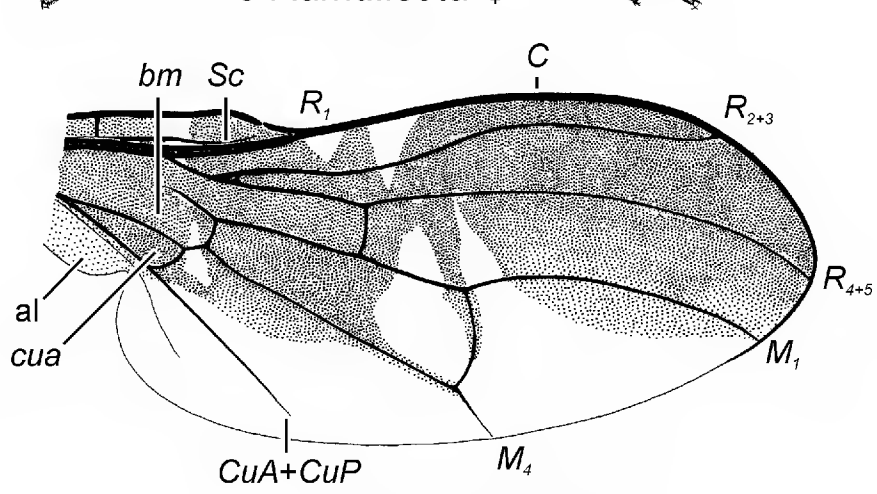
4 *Ramuliseta* ♀



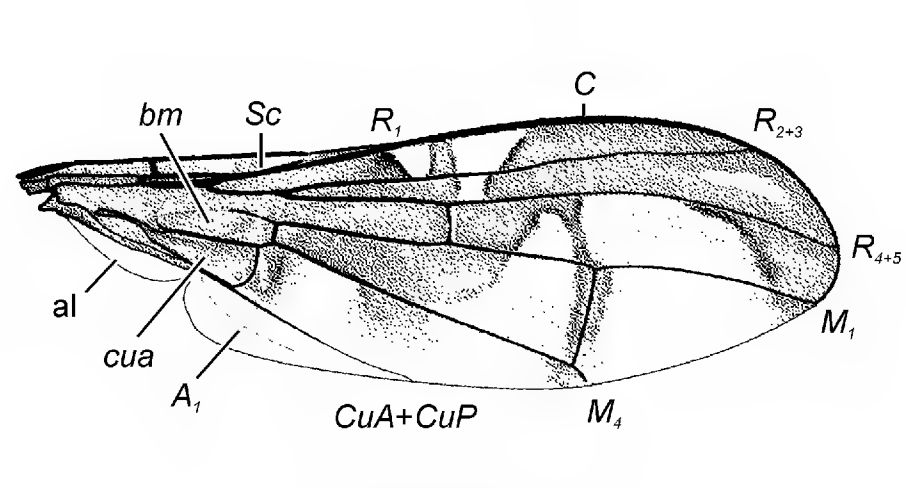
5 *Ramuliseta* ♀



6 *Ramuliseta* ♀



7 *Ramuliseta* ♀



8 *Ramuliseta* ♀

Figs 73.2–8. Heads, habitus and wings of Ctenostylidae: (2) head of *Ramuliseta palpifera* Keiser, lateral view ♂; (3) same, anterior view ♂; (4) same ♀; (5) habitus of *Ramuliseta* sp., lateral view ♀; (6) wing of *R. madagascariensis* Hennig, dorsal view ♀; (7) same, *R. palpifera*; (8) same, *R. dolini* Korneyev. Figs 2, 3 (Barraclough 1998, figs 6, 7), Fig. 6 (Hennig 1960, fig. 1).

Abbreviations: A_1 – first branch of anal vein; al – alula; ar – arista; *bm* – basal medial cell; *C* – costal vein; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; fr – frons; M_1 – first branch of media; M_4 – fourth branch of media; plp – palpus; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *Sc* – subcostal vein.

Ctenostylidae are usually recognised by the subequal size of the head and thorax, long slender legs and patterned wings. They are readily distinguished from all other families by the lack of both a proboscis and ocelli. Long-legged Pyrgotidae (see Chapter 72), in which ocelli are also lacking and which have wing cell *cua* without a posteroapical extension (lobe), have a functional proboscis, although in *Toxopyrgota* Hendel this is somewhat reduced. Additionally, in Afrotropical Pyrgotidae the female aculeus is stiletto-like, lacking long setae in the basal part (modified tergosternite 8), or acute apical portion (modified cerci). In Agromyzidae (see Chapter 86), which have a similarly reduced apical section of the subcostal vein (*Sc*) and basal section of vein M_1, the wings are hyaline, the tibiae are setulose dorsally and the proboscis and ocelli are normally developed.

Biology and immature stages

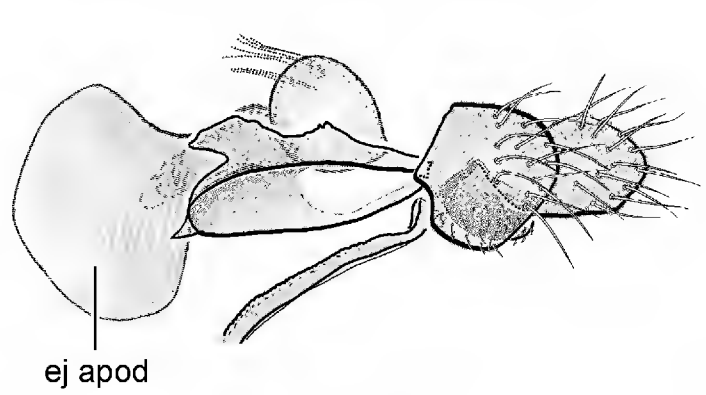
Virtually nothing is known regarding the biology of Ctenostylidae. Adults of the Oriental *Ramuliseta ashleyi* Barraclough, 1998, were collected shortly after dusk at a mercury-vapour light on a lake shore in Sulawesi, Indonesia by A.H. Kirk-Spriggs (Barraclough 1998). Adult females lack a piercer at the apex of the telescopic ovipositor, unlike females of closely related Pyrgotidae and Tephritidae: Tachiniscinae (which have a short and sharp, strongly modified tergosternite 8; the so-called "aculeus"), but may also be parasitoids that disperse larvae in the vicinity of or on potential hosts, rather than ovipositing directly into the host's body. Dissected females often have the abdomen full of small eggs containing first-instar larvae (Korneyev 2010: 964, 968). Adult flies have rudimentary, or entirely lack, mouthparts and are aphagous. Larvae and puparia have not been described.

Economic significance

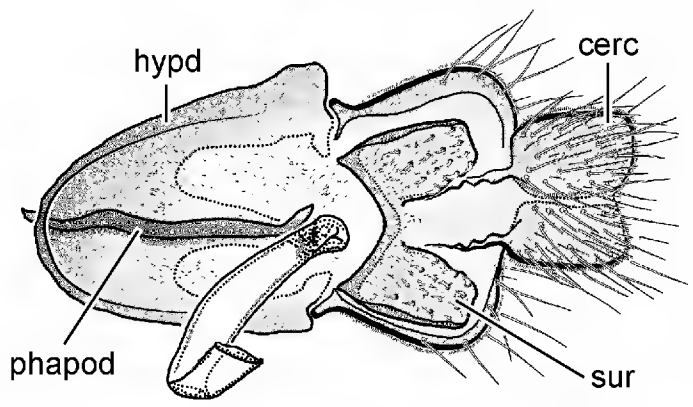
The Ctenostylidae have no known economic importance. There are no records involving any species in agricultural, medical, veterinary or forensic works.

Classification

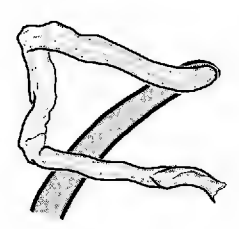
Monophyly of the Ctenostylidae is supported by the reduction of the basal part of wing vein *M* (cell *bm* open



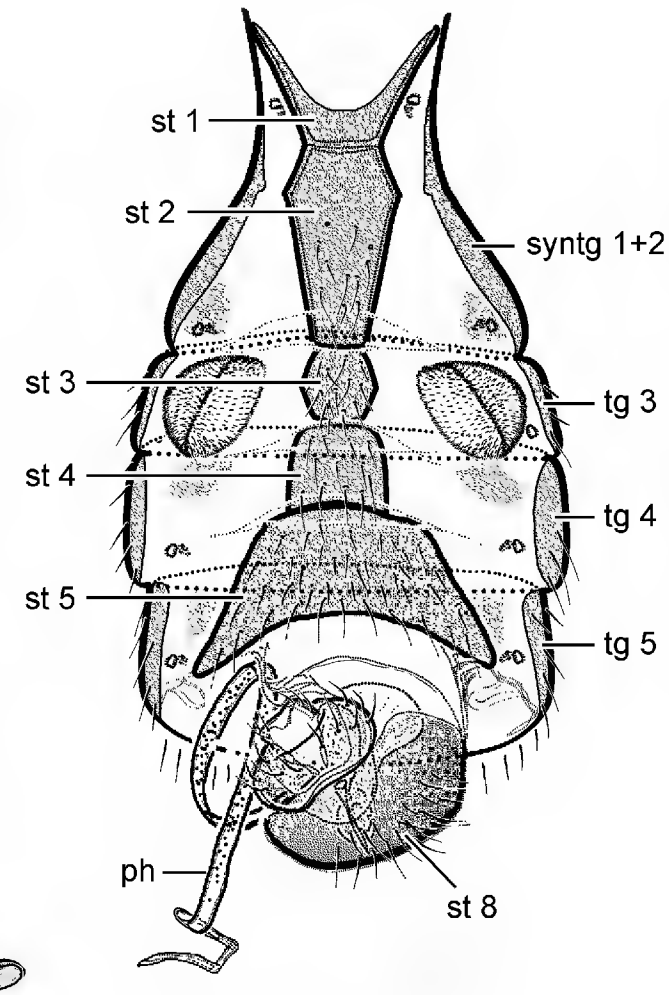
9 *Furciseta* ♂



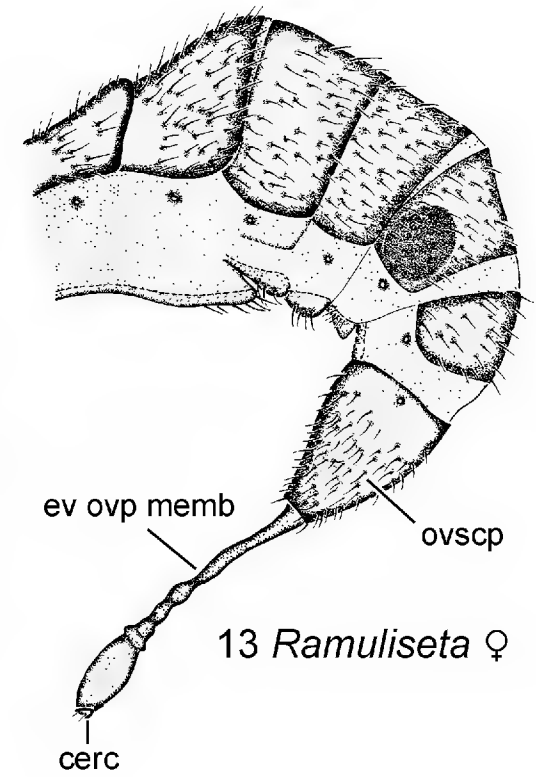
10 *Furciseta* ♂



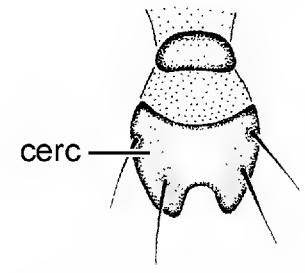
11 *Furciseta* ♂



12 *Furciseta* ♂



13 *Ramuliseta* ♀



14 *Ramuliseta* ♀

Figs 73.9–14. Male terminalia and male and female abdomen of Ctenostylidae: (9) male terminalia of *Furciseta plaumanni* (Hennig), lateral view (apical part of distiphallus not illustrated) (non-Afrotropical); (10) same, ventral view; (11) same, apical part of distiphallus, ventral view; (12) same, male abdomen, ventral view; (13) female abdomen of *Ramuliseta palpifera* Keiser, lateral view; (14) same, female cerci, ventral view. Figs 9–12 (Korneyev 2010, figs 19–21, 23), Figs 13, 14 (Barraclough 1994, figs 3, 5).

Abbreviations: cerc – cercus; ej apod – ejaculatory apodeme; ev ovp memb – eversible ovipositor membrane; hypd – hypandrium; ovscp – oviscape; ph – phallus; phapod – phallapodeme; st – sternite; sur – surstylus; syntg – syntergite; tg – tergite.

anterobasally), the branched female antennal arista (unique synapomorphies), as well as by the vestigial proboscis and absence of ocelli. They were originally treated as the subfamily Lochmostyliinae of Pyrgotidae by Hendel (1934) and Aczél (1956), but were excluded from the Pyrgotidae by McAlpine (1990). Korneyev (2001) suggested that Ctenostylidae belong in the Tephritoidea and are related to the Platystomatidae + Pyrgotidae + Tephritidae group of families. Further studies of the male terminalia of Neotropical *Furciseta* have confirmed that Ctenostylidae indeed belong in this group of families. In recent molecular phylogenies, the Ctenostylidae are nested within Platystomatidae + Pyrgotidae + Tephritidae (Han & Ro 2016; Wiegmann *et al*. 2011).

A catalogue of the Ctenostylidae of the world was published by Pereira-Colavite & Mello (2014).

Identification

Barraclough (1994, 1995, 1998), Yang (1995) and Korneyev (2001) reviewed the Old World species, whereas Raphael *et al*. (2009), Korneyev (2010) and Câmara & Rafael (2013) provided additional data on New World ctenostylids. Identification keys to Old World Ctenostylidae are provided by Hennig (1960), Barraclough (1994, 1998) and Korneyev (2001). Afrotropical species were keyed by Korneyev (2015). Ctenostylidae are best micro-pinned in the field for later double-mounting (see Chapter 2).

Synopsis of the fauna

Currently the family comprises at least 14 described species and 7 nominal genera globally, of which six described (and 2–3 undescribed) species occur in the Old World, including three *Ramuliseta* species occurring in the Afrotropical Region and three genera with eight to nine species recorded in the Neotropical Region. *Ramuliseta* is the only genus recorded from the Afrotropics.

***Ramuliseta* Keiser.** A genus of four described species occurring in the Afrotropical and Oriental Regions, with three species in the Afrotropical Region. The type species, *R. palpifera* Keiser, 1951 (Figs 3–5, 7, 13–14), is widespread in Southern Africa and the Oriental Region and both *R. madagascarensis* Hennig, 1960 (Fig. 6) and *R. dolini* Korneyev, 2015 (Figs 1, 8) are recorded from Madagascar and are known from females only (Korneyev 2015). The immature stages remain unknown. An identification key to the three Afrotropical species was provided by Korneyev (2015).

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LAUXANIIDAE 74

(Lauxaniid Flies)

Stephen D. Gaimari and Raymond M. Miller

Fig. 74.1. Male of *Homoneura* sp. (Madagascar) (photograph © S.A. Marshall).

Diagnosis

Small- to moderately large-sized (body length: 2–11 mm) acalyptrate flies; compact-bodied (Figs 1–3, 5–11) or elongate (Fig. 4); varied in colour patterns, uniform or simple (Figs 5, 7, 28, 35, 42), or more often with markings and maculae (Figs 27, 29), fasciae (Figs 1, 6, 26, 36, 46, 47), reticulating patterns (Figs 43, 44) or metallic (Figs 4, 10, 32, 33, 41, 49); wings similarly varied, from hyaline (Figs 5, 40, 41, 53, 55, 56), to variously marked with maculae (Figs 1, 8, 9, 31), bands (Figs 10, 32), or reticulating patterns (Figs 2, 27, 50, 51, 54).

Head with postocellar setae convergent to cruciate (Figs 18, 20), rarely absent; ocellar setae proclinate, divergent to subparallel, small and setula-like (Figs 21, 37) to strong (Figs 15, 17), rarely absent (Fig. 25); orbital plate with 2 fronto-orbital setae (anterior seta sometimes minute (Fig. 19) or small (Fig. 38)), usually reclinate (Figs 14, 23), but anterior seta sometimes slightly (Fig. 21) to strongly (Figs 20, 22, 28) inclinate; lunule small, narrowly exposed and bare; face various, from slightly concave or flat (Figs 17, 23, 24, 49), to convex or bulging (Figs 16, 20, 25, 36, 45), sometimes receding (Figs 4, 12, 18, 19, 40); subgena usually thin, inconspicuous (Fig. 14), but

occasionally enlarged, bulging (Figs 15, 16); oral vibrissa absent, although oral margin sometimes with row of elongated setae (Figs 21, 40).

Thorax with mesonotum setulose, occasionally virtually bare; with 2–4 dorsocentral setae (rarely 1), either posteriorly located (0 + 2 (Fig. 34), 0 + 3 (Figs 27, 28, 39, 42)) or evenly distributed with 1 presutural (1 + 2 (Figs 37, 47), 1 + 3 (Figs 29, 44, 46, 48)); prescutellar acrostichal seta usually present, sometimes with additional acrostichal setae in row (Figs 29, 35) and/or with rows of acrostichal setulae; scutellum with 2 pairs of setae; anepisternum setulose, with 1 strong seta near posterior margin, sometimes with an additional seta (Fig. 35) or setae; katepisternum setulose, with 1–2 setae dorsally. Wing (Figs 50–56) with costal vein (*C*) unbroken, weakened beyond vein R_{4+5} and ending at vein M_1, usually (except in *Drepanephora* Loew (Fig. 51)) with stout black spinules on anterodorsal surface ending slightly beyond apex of vein R_{2+3} in Lauxaniinae (Fig. 56) or continued to vein R_{4+5} in Homoneurinae (Figs 53, 54), although fine setulae often continue around wing beyond spinules; subcostal vein (*Sc*) complete, separated from vein R_1; cell *cua* small with rounded apex; vein *CuA+CuP* usually short, not reaching wing margin; membrane various, from hyaline to darkened crossveins to intricately patterned, irrorated or banded. Each leg usually with preapical dorsal tibial seta.

Abdomen short, stout to elongate and tapering; male tergite 6 sometimes fused with syntergosternite 7 + 8, with terminalia recurved below; syntergite 7 + 8 saddle-shaped (broad medially, narrowing laterally) (Fig. 62), often fused into syntergosternite (Fig. 57); epandrium simple, saddle-shaped (Fig. 59), or divided anteromedially; surstylus large (Fig. 71) or small (Fig. 62), articulated with epandrium, sometimes with ornamentation or hooks, or subdivided into inner and outer (Fig. 59); pregonite rarely well-developed, often absent; postgonite present and often highly modified, sometimes asymmetrical in length and shape; phallus variable, large or small, often recurved, with lobes, flanges, striations or ridges, occasionally membranous and indistinct; phallapodeme short or elongated (Figs 60, 61, 63–65); ejaculatory apodeme simple; female sclerites of segment 7 separate, or forming complete sclerotised ring (syntergosternite 7) surrounding terminalia; sternite 8 variously modified, large or small; with distinct epiproct and hypoproct and short cerci; spermathecae globular, in conformation 1 + 2, or occasionally 2 + 2 or 1+1.

Figs 74.2–5. Photographs of living Afrotropical Lauxaniidae: (2) *Cestrotus* sp. (sex unknown) (Tanzania); (3) *Homoneura* sp. ♀ (Tanzania); (4) *Lauxania* sp. ♂ (Madagascar); (5) *Sapromyza* sp. ♀ (South Africa). Figs 2–5 (photographs © S.A. Marshall).

Egg white, ovoid in dorsal view, sometimes banana-shaped in lateral view, or flattened on dorsal surface; anteriorly with distinct tubercle shielding apical micropyle; posteriorly with knob-like swelling or constricted tubercle; chorion with distinct longitudinal ridges (often connected by transverse septa, occasionally with spicules along ridges), often with pitted or reticulated patterns at each pole.

Third-instar larvae musciform (Figs 72, 73, 76), tapering slightly anteriorly, less so posteriorly (Fig. 73), often compressed dorsoventrally; outer integument translucent (Figs 72, 73); oral area with multiple rows of spicules (Fig. 79); all segments with bands of spinules anterodorsally, segments 3–12 with similar bands of spinules anteroventrally, in addition to ventral creeping welts (Fig. 76); often with other spinules on body surface and/or near

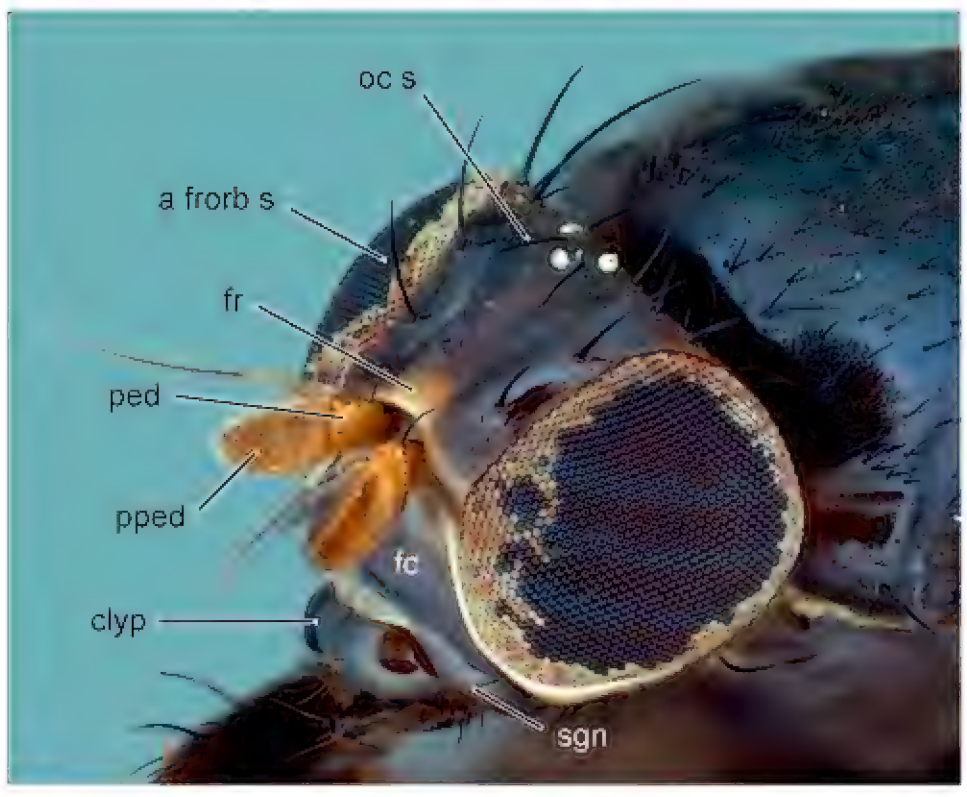
Figs 74.6–11. Photographs of living female Afrotropical Lauxaniidae: (6) *Homoneura* sp. (Tanzania); (7) same (Tanzania); (8) same (Tanzania); (9) same (Tanzania); (10) same (Madagascar); (11) same (Ghana). Figs 6–10 (photographs © S.A. Marshall), Fig. 11 (photograph © S.D. Gaimari).

anal plate; segment 12 with up to 3 pairs of fleshy lobes or tubercles dorsolaterally, laterally and ventrolaterally (Fig. 80); prothoracic spiracles arranged fan-like, with 4–14 papillae at end of spiracular stalk (Fig. 77), or with 11–19 finger-like papillae in cluster at end of stalk; posterior spiracles on short, separate, usually darkened, posteriorly directed tubular mountings on terminal segment (Figs 72, 76, 80), with each spiracular plate circular, bearing 3 ovoid to elongate-oval spiracular openings in radiating pattern from slightly divergent to right-angled, with four 6–20 branched peristigmatic tufts (Fig. 81); cephaloskeleton (Figs 78, 79) with mouthhook slender to stout, with or without accessory tooth, but usually with small basal "window"; dental sclerite and ventral pharyngeal ridge present; labial sclerite arched, with slender posteriorly directed rod-like rami medial to parastomal bar; parastomal bar present, small, not fused apically or to epistomal sclerite; intermediate sclerite and basal sclerite separate, with left and right dorsal cornua connected by dorsal bridge; dorsal cornu slender, usually shorter and narrower than ventral cornu; ventral cornu often with "window" along dorsal margin.

Puparium (Figs 74, 75) ovoid, tapering slightly more posteriorly than anteriorly; convex dorsally, flattened ventrally; anterior end dorsoventrally flattened to produce lateral ridge; surface often covered with white calcareous deposit secreted from anus prior to pupariation.

12 *Cainohomoneura* ♀

13 *Cainohomoneura* ♀



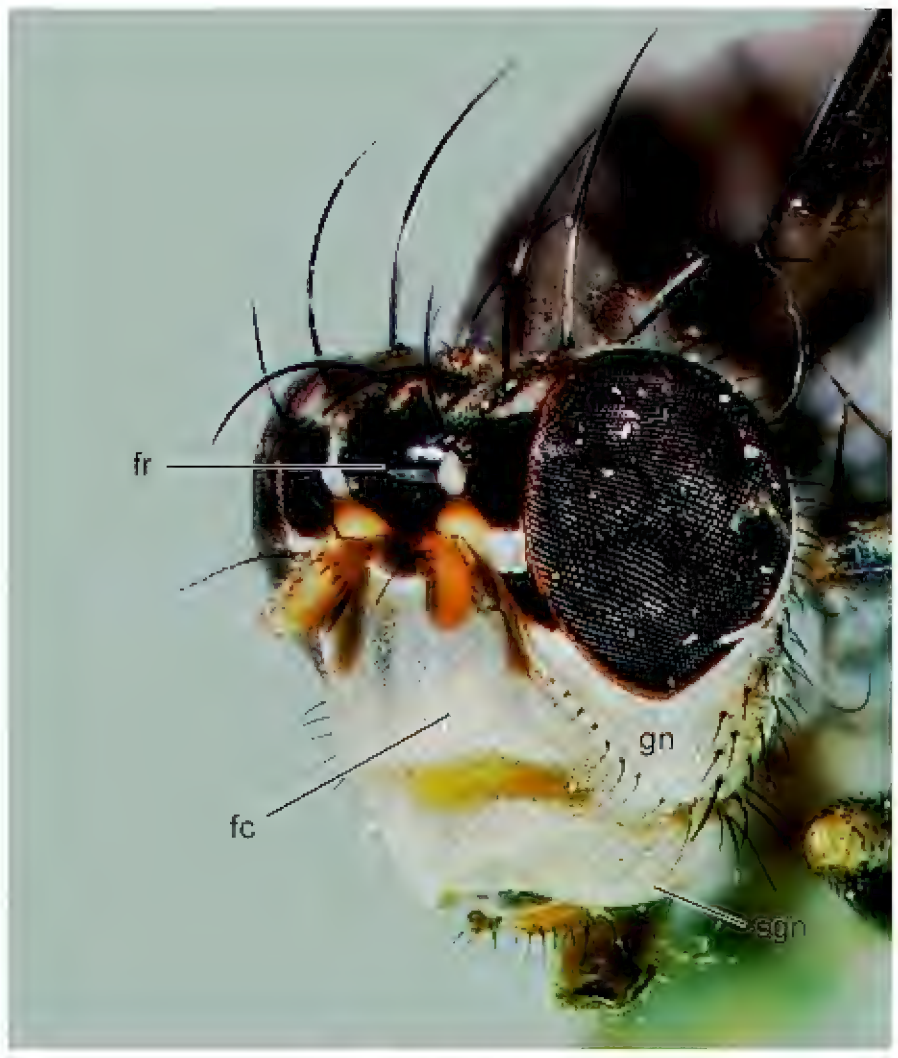
14 *Calliopum* ♀

15 *Cestrotus* ♂

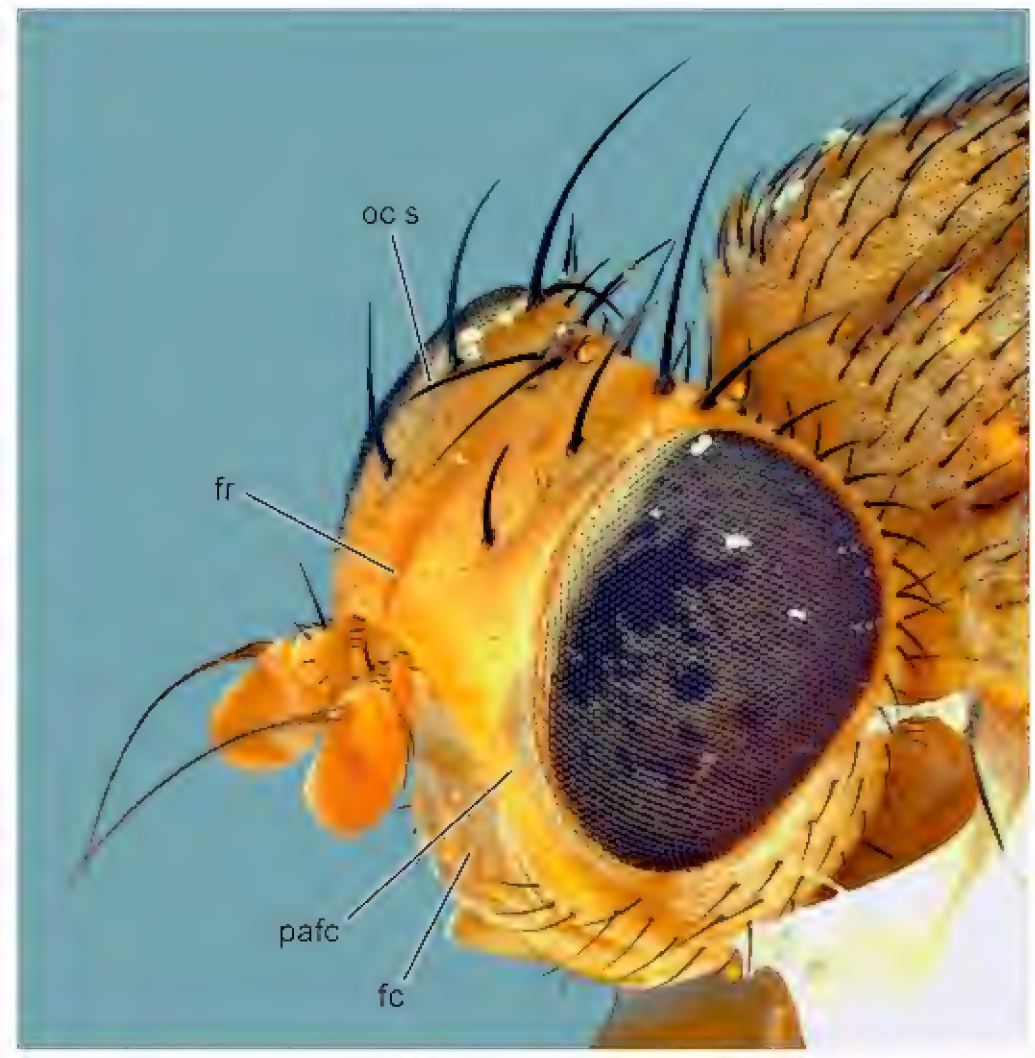
Figs 74.12–15. Heads of Lauxaniidae: (12) *Cainohomoneura delta* Stuckenberg, lateral view ♀; (13) same, oblique anteroventral view; (14) *Calliopum* sp., lateral oblique view ♀; (15) *Cestrotus* sp., lateral oblique view ♂.

Abbreviations: a frorb s – anterior fronto-orbital seta; clyp – clypeus; fc – face; fc car – facial carina; fr – frons; oc s – ocellar seta; ped – pedicel; pped – postpedicel; sgn – subgena.

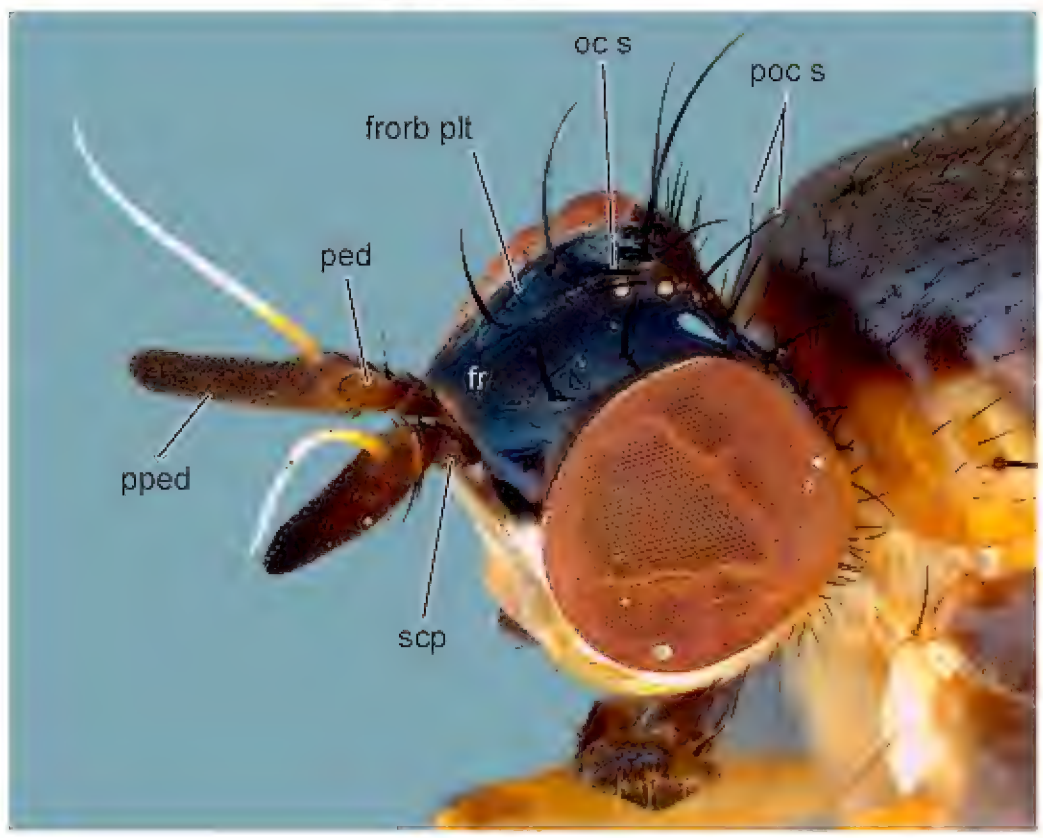
Adult Lauxaniidae are usually recognised by: the unbroken costal vein (*C*), with the subcostal vein (*Sc*) being entire and separate from wing vein R_1; the presence of 2 fronto-orbital setae, the posterior of which is invariably strong and reclinate, the anterior seta has more variation, being either strong or weak (usually strong), reclinate or inclinate (usually reclinate); the presence of converging or cruciate postocellar setae; the presence of a preapical dorsal tibial seta on each tibia; and



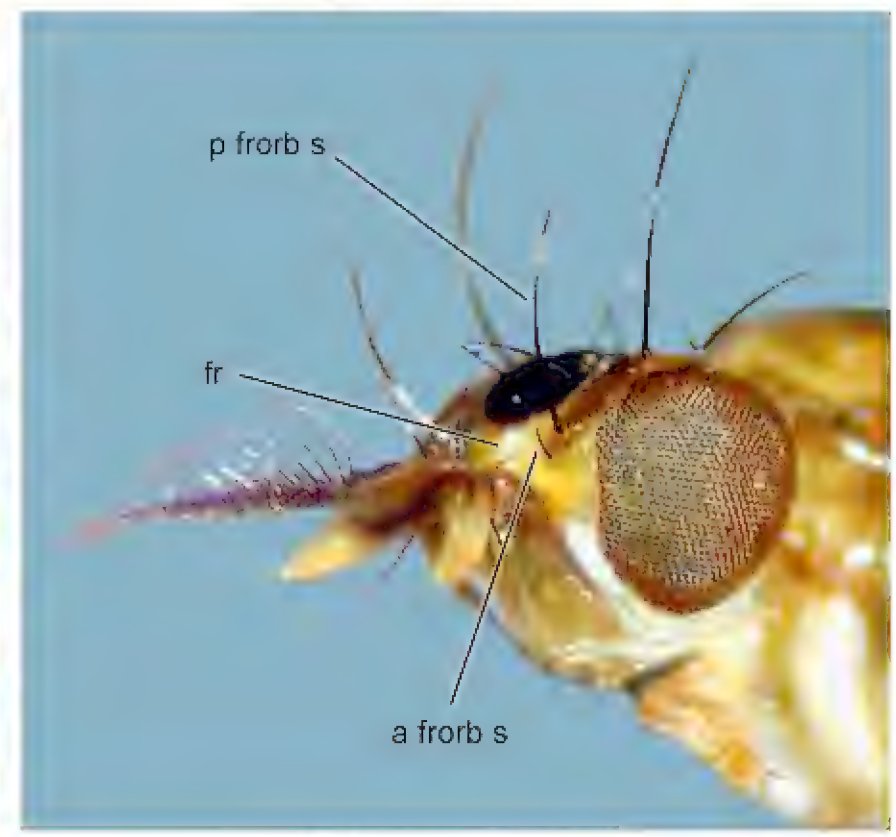
16 *Cestrotus* ♂



17 *Dyticomyia* ♀



18 *Lauxania* ♀



19 *Neogeomyza* ♂

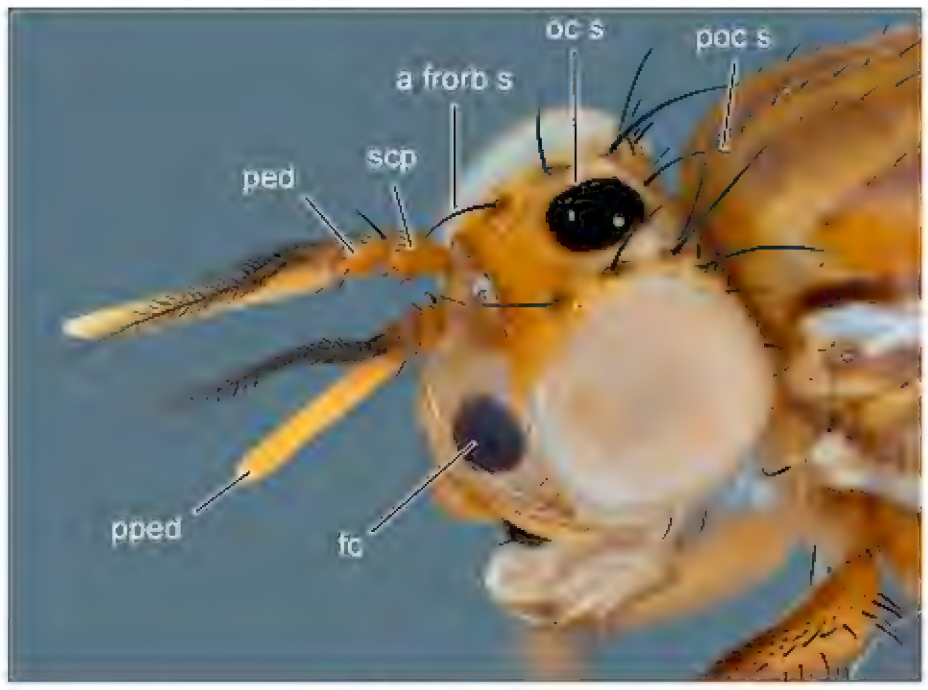
Figs 74.16–19. Heads of Lauxaniidae: (16) *Cestrotus* sp., anterolateral view ♂; (17) *Dyticomyia oraria* Stuckenberg, lateral oblique view ♀; (18) same, *Lauxania* sp.; (19) *Neogeomyza stenoptera* (Stuckenberg), anterolateral view ♂.

Abbreviations: a frorb s – anterior fronto-orbital seta; fc – face; fr – frons; frorb plt – fronto-orbital plate; gn – gena; oc s – ocellar seta; p frorb s – posterior fronto-orbital seta; pafc – parafacial; ped – pedicel; poc s – postocellar seta; pped – postpedicel; scp – scape; sgn – subgena.

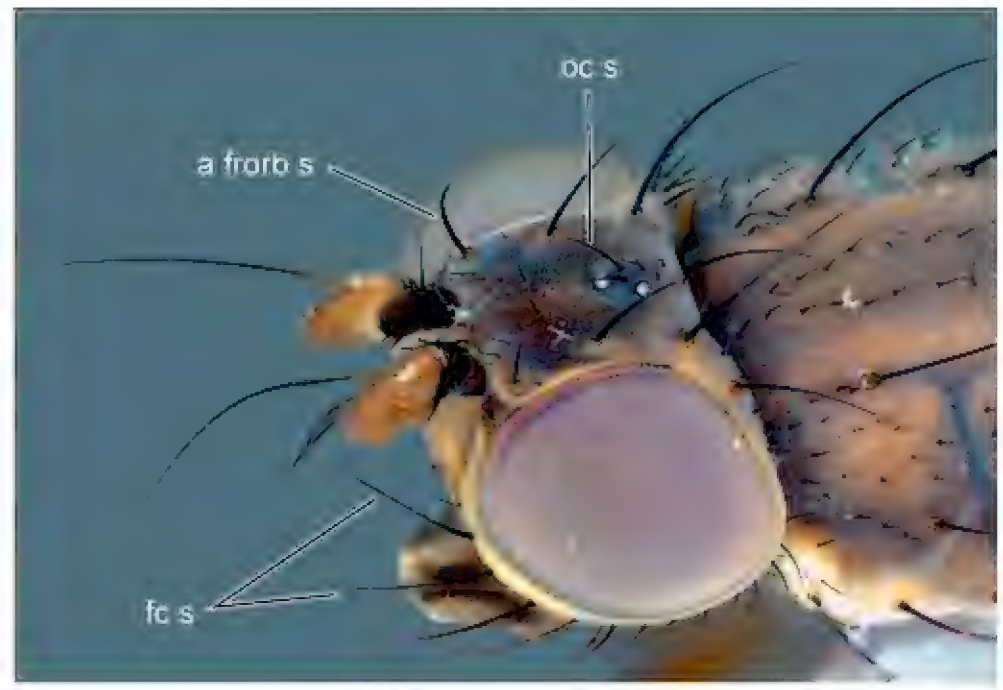
the presence of a strong anepisternal seta along the posterior margin. Celyphidae (see Chapter 75) are very closely related, if not part of this family and are distinguishable by the enlarged scutellum extending over the entire abdomen. The subfamily Chamaemyiinae of the related family Chamaemyiidae (see Chapter 76) are also very similar, being easily distinguished by the lack of a dorsal preapical seta on the tibiae, lack of black costal spinules on the wing and presence of a prescutellum (absent in Lauxaniidae); the subfamily Leucopinae is also separable based on these characteristics, but also differs in lacking one or both fronto-orbital setae.

Biology and immature stages

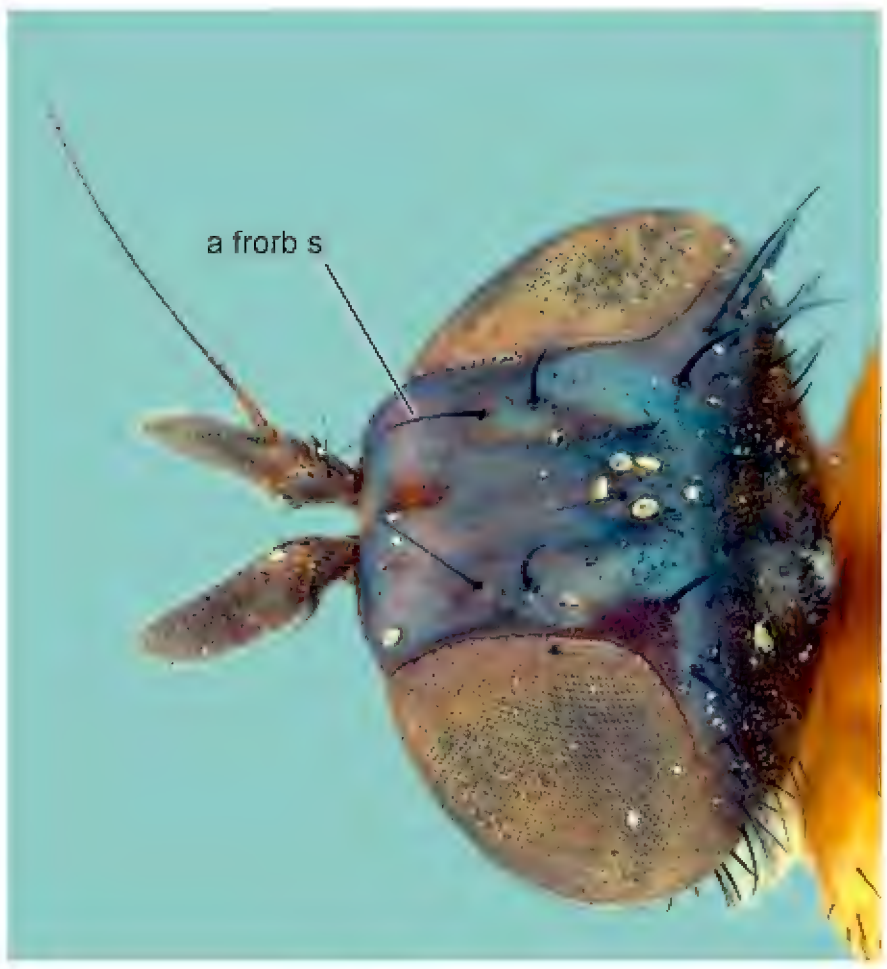
Adult lauxaniids are fungal grazers on leaves (Broadhead 1984, 1989) and display related mouthpart modifications. Attesting to their biological importance, lauxaniids are probably among the more important dipterans responsible for turnover of enormous quantities of organic litter in the tropics, likely playing a significant role in the healthy functioning of tropical ecosystems (Freidberg & Yarom 1990). In addition, despite their generalisation as saprophages, there are many examples of specialisation to different media and feeding strategies.



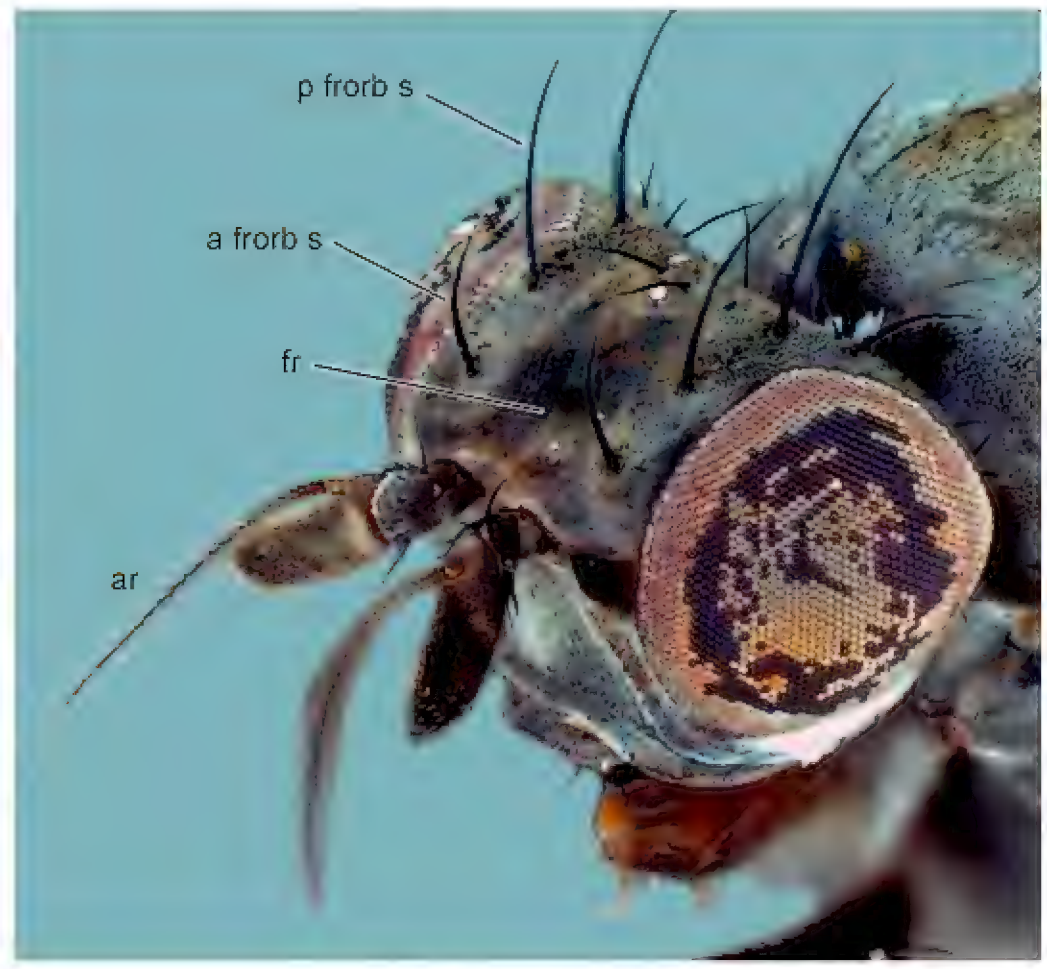
20 *Pachycerina* ♂



21 *Prochaetops* ♂



22 *Prosamyza* ♂



23 *Sapromyza* ♀

Figs 74.20–23. Heads of Lauxaniidae: (20) *Pachycerina vaga* Adams, lateral oblique view ♂; (21) same, *Prochaetops* sp.; (22) *Prosamyza viridiventris* Stuckenberg, dorsal view ♂; (23) *Sapromyza* sp., lateral oblique view ♀.

Abbreviations: a frorb s – anterior fronto-orbital seta; ar – arista; fc – face; fc s – facial setae; fr – frons; oc s – ocellar seta; p frorb s – posterior fronto-orbital seta; ped – pedicel; poc s – postocellar seta; pped – postpedicel; scp – scape.

Larval lauxaniids are widely documented as saprophages (Miller 1977*a*), feeding in a diverse array of decaying plant matter, likely consuming associated micro-organisms, fungi, bacteria, or yeasts (Miller & Foote 1976). One species is known to feed in flower heads of the botanical family Asteraceae in Brazil; although saprophagy could not be ruled out; these data suggested a phytophagous existence (Silva & Mello 2008). The Afrotropical genus *Proteaphila* Davies & Miller is closely associated with the botanical genus *Protea* (Proteaceae) (Davies *et al.* 2012), but the biological relationship is not yet known.

Miller (1977*a*) summarised the known larval biologies for 70 species in 21 genera and subgenera, reporting that more than half bred in fallen leaves of deciduous trees (= leaf litter). Of these, only *Homoneura* Wulp (three subgenera) (Hardy & Delfinado 1980: 133; Miller 1977*a*; Sasakawa & Ikeuchi 1982) and *Tricholauxania* Hendel (de Meijere 1906) appear restricted to this medium. Interestingly, among leaf litter-feeders there is a subspecialisation to feed in decaying mesophyll tissues between the upper and lower epidermis, as leaf-miners of fallen leaves (Ferrar 1987: 203; Hering 1951: 45; Miller 1977*a*). Of the relative minority of non-leaf litter-feeders, several genera and subgenera have species that are nidicolous, feeding on decaying matter in birds' nests, including *Pachycerina* Macquart, *Poecilominettia* Hendel and *Pseudocalliope* Malloch (Davies & Miller 2009; Hicks 1953; Miller & Foote 1975), the *Minettia* Robineau-Desvoidy subgenus *Frendelia* Collin (Armstrong 1953), the *Meiosimyza* Hendel subgenus *Lyciella* Collin (Miller 1977*a*; Thienemann 1926), "*Sapromyza*" (*sensu* Colless & McAlpine 1970: 724) and *Calliopum* Strand (Collin 1933; Miller 1977*a*), or within mammalian nests, such as *Minettia* (Séguy 1946), *Sapromyza* Fallén (Lyayster 1967) and *Pseudogriphoneura* Hendel (Miller 1977*a*). Other known feeding sites include rotting fungus (Chandler 2010: 438), under bark of rotting tree stumps (Collin 1948; de Meijere 1909; Laurence 1952) and within rotting gymnosperm cones (Keen 1958; Miller 1977*a*) and club tops (Miller 1977*a*). Just prior to pupariation, larvae of some species first excrete their gut contents and then cover themselves with a calcareous anal secretion originating from large extensions of the Malpighian tubules that hardens after being smeared over the body surface (Miller & Foote 1975). At least one species of *Pseudocalliope* forms a mud-and-fiber cocoon around its puparium (Miller & Foote 1975).

Morphology of the immature stages is known for a few species, although none of these are Afrotropical. Foote (1991: 833) suggested that many larval lauxaniids are difficult, if not impossible, to separate from other saprophagous acalyptrates, although considerable progress has been made with respect to lauxaniid immatures. The most recent studies were undertaken by Semelbauer & Kozánek (2011, 2012, 2013, 2014), who provided extensive descriptions and numerous figures for all immature stages of 30 Palaearctic species in the following 13 genera and subgenera, a few of which have Afrotropical species: *Aulogastromyia* Hendel, *Calliopum*, *Cnemacantha* Macquart, *Homoneura sensu stricto*, *Lauxania* Latreille, *Meiosimyza*, *Minettia sensu stricto*, *Peplomyza* Haliday, *Poecilolycia* Shewell, *Pseudolyciella* Shatalkin, *Sapromyza sensu stricto*, *Sapromyza* (*Sapromyzosoma* Lioy) and *Tricholauxania* Hendel.

The eggs are described and illustrated for two species of the non-Afrotropical subfamily Eurychoromyiinae (Gaimari & Silva 2010*b*). Prior to this, details and extensive figures were provided by Miller & Foote (1976) for all stages and instars for species in the following genera and subgenera: *Camptoprosopella* Hendel, *Homoneura* (*Tarsohomoneura* Hendel), *Melanomyza* Malloch, *Minettia* (*Frendelia*), *Minettia sensu stricto*, *Poecilolycia*, *Poecilominettia* and *Pseudocalliope*. Ferrar (1987: 203) had summarised the knowledge of lauxaniid immatures up to that time. Few other studies have dealt with morphology of lauxaniid immatures, so there is still much to learn as this represents a small subset of the known genera in the family.

Economic significance

No species of economic significance are currently known.

Classification

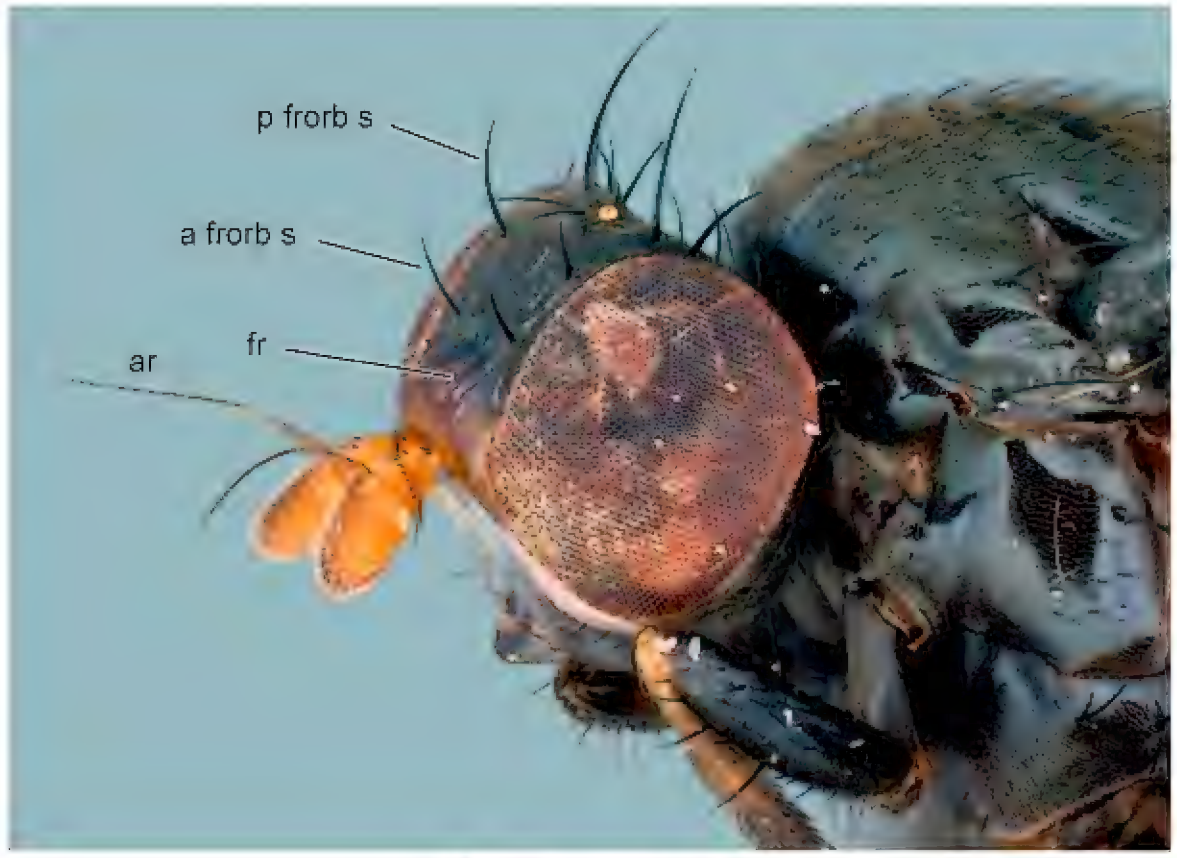
Frey (1941: 23) was the first to recognise subfamilial divisions of the family, adding Homoneurinae and Minettiinae, but the subfamilial names were without descriptions. Stuckenberg (1971) validly proposed the subfamily Homoneurinae for a (potentially) monophyletic group of genera, based on the presence of costal setulae extending to the apex of wing vein R_{4+5}. Stuckenberg (1971) also noted that most species in this subfamily possess an anteroventral ctenidium (= comb) on the fore femur, while few non-homoneurines exhibit this state. Shewell (1977: 183) later added the presence of one or two extra mid tibial spurs (actually not true spurs, but stout apical setae), as further support for the subfamily; also proposing the paraphyletic subfamily Lauxaniinae for the remainder of the family, based on costal setulae ending just beyond the apex of wing vein R_{2+3} and a single mid tibial spur. The conditions cited for Lauxaniinae are clearly plesiomorphic and are likely part of the groundplan for the entire Muscomorpha (McAlpine 1989: 1446) and both Stuckenberg (1971) and Shewell (1977: 182) acknowledged the likely paraphyly for the group. Within this group, two tribes have been proposed for compact groups of genera, including the Trigonometopini (Becker 1905: 41) and Noonamyiini (Sasakawa 1995); the former of which was also treated at this level by Papp (2007, 2008), who also discussed the need to define smaller monophyletic groups of genera to deal with the paraphyly of Lauxaniinae. Within Homoneurinae, Kim (1994) presented phenetically-based dendrograms for the Australian representatives, resulting in several new genera, but it must be noted that monophyly was apparently not a criterion in their definitions and in their separation from *Homoneura* or other genera. No additions or changes to the suprageneric classification were proposed.

Although Lauxaniidae is among the largest families of Acalyptratae, the internal classification of the family is in its infancy. The monophyly of the family is supported by several autapomorphies (McAlpine 1989: 1446), including: the male accessory glands forming a dense tangle, due to repeated branching (Sturtevant 1925, 1926), the phallus being reduced to a rigid tubular process and the lunule being unexposed. Within the Lauxanioidea, Lauxaniidae is clearly separated from Chamaemyiidae, but the monophyly of the family relative to Celyphidae and non-Afrotropical Eurychoromyiidae has been contentious and so the last mentioned was revised to subfamily status (Gaimari & Silva 2010*b*), with a thorough discussion of the history of its classification.

Although lauxaniids are uncommon in the fossil record, several species have been described from Eocene/Oligocene Baltic and Chinese ambers (Hennig 1965; Hong 1981: 143). In addition, no less than 15 undescribed species from 24 specimens in Dominican amber are being described by the writers, all in extant New World genera.

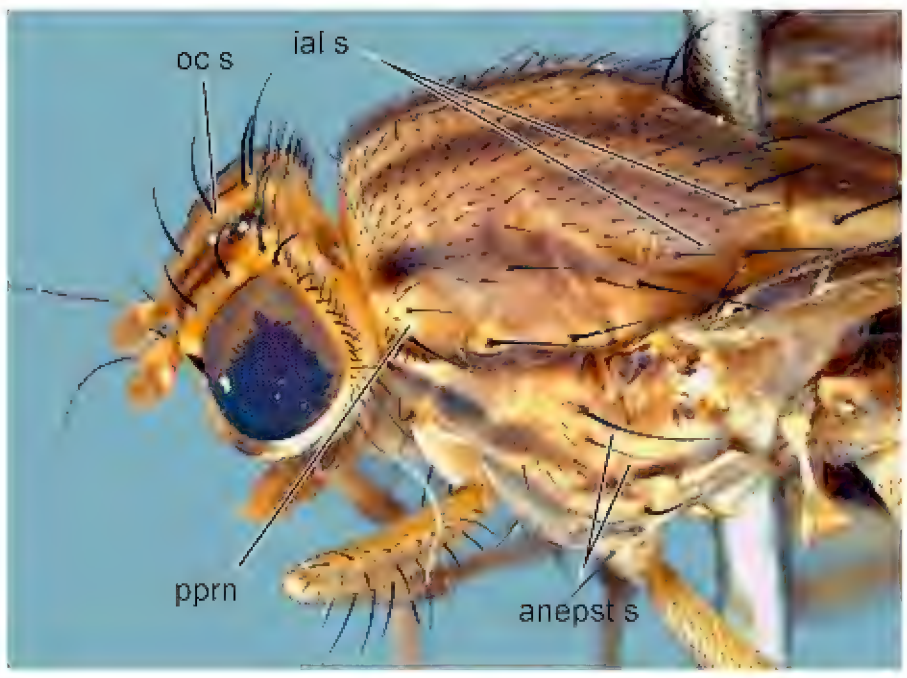
Identification

The literature for identifying the described species of Lauxaniidae is sparse and many species remain undescribed worldwide, particularly in the Old and New World tropics. There are few modern synthetic works at the species-level. For genera, the most significant work was the monumental review of all Old World genera by Stuckenberg (1971), including an identification key to genera. Gaimari & Silva (2010*a*: 975) provided an identification key to all genera in the New World, which supplements the identification key to Nearctic genera by Shewell (1987: 954). For the Palaearctic Region, Papp & Shatalkin (1998: 389) provided an identification key to genera and Shatalkin (2000) further provided an overview of all Palaearctic genera, with identification keys to the described species of that region; Schacht *et al*. (2004) provided updates and translation into English for these keys. For the Nearctic Region, Miller (1977*b*, *c*) revised the fauna of the large genus *Homoneura* and Pérusse & Wheeler



24 *Sapromyza* ♀

25 *Xangelina* ♂



26 *Afrominettia* ♀

27 *Cestrotus* ♀

Figs 74.24–27. Heads and thoraces and heads of Lauxaniidae: (24) head and thorax of *Sapromyza* sp., anterolateral view ♀; (25) head of *Xangelina* sp., anterolateral view ♂; (26) head and thorax of *Afrominettia* sp., dorsolateral view ♀; (27) same, *Cestrotus* sp., dorsal view ♀.

Abbreviations: a frorb s – anterior fronto-orbital seta; anepst s – anepisternal setae; ar – arista; fc – face; fr – frons; ial s – intra-alar setae; oc s – ocellar seta; p frorb s – posterior fronto-orbital seta; pprn – postpronotum.

(2000) revised the fauna of *Lauxania*, both of which have Afrotropical representatives. For the Oriental Region, the many works of Sasakawa (e.g., 1992, 2001) and colleagues (e.g., Sasakawa & Ikeuchi 1982), have provided faunistic and revisionary studies, particularly for the Homoneurinae, in that highly species-rich region. In Australasia, Kim (1994) revised the fauna of Homoneurinae, providing identification keys to the genera and species of that region. For the Afrotropical Region, Stuckenberg (1971) has been the primary resource for identifying genera and subgenera and Miller (1980: 603) compiled all the known genera with their species and distributions.

Most descriptions for Afrotropical taxa were made in a piecemeal way, with only six authors describing 10 or more species each, including Curran (1938; 14 species in six genera), Davies & Miller (2008, 2009 and Davies *et al*. 2012; 14 species in three genera), Lamb (1912; 11 species in four genera, all from Seychelles), Loew (1852, 1862; 13 species in six genera) and Stuckenberg (1963, 1971; 10 species in nine genera). Several of these included identification keys to species, but most species are not included in any keys and no synthetic Afrotropical work exists. It is noteworthy that the mainstay authors for lauxaniid taxa, J.R. Malloch and F. Hendel, had only a combined seven described Afrotropical species and only one described endemic or near endemic genus – *Katalauxania* Hendel. Of the more than 300 species J.R. Malloch described worldwide, only one was Afrotropical. This lack of attention paid to the Afrotropical Region by the major lauxaniid workers is likely the reason the fauna appears to be depauperate in terms of genus and species diversity.

At the genus-level, Stuckenberg (1971) has been the primary resource for identifying the species in the monotypic (*Cainohomoneura* Stuckenberg, *Dyticomyia* Stuckenberg, *Nimettia* Stuckenberg, *Procestrotus* Stuckenberg, *Prosamyza* Stuckenberg and *Teratolauxania* Stuckenberg) and some small (*Noonamyia* Stuckenberg and *Zanjensiella* Stuckenberg) genera. Several other works describe and provide identification keys for the species of certain genera and subgenera, including Papp's (2008) treatment of the subgenus *Sauteromyia* Malloch of the genus *Diplochasma* Knab, Davies & Miller (2008, 2009) treatments of *Parapachycerina* Stuckenberg and *Pachycerina* respectively and Davies *et al*. (2012) description and treatment of *Proteaphila*.

The following identification key attempts to update the genus and subgenus identification resources for the Afrotropics and fix some issues in Stuckenberg (1971), overall providing an entry point for a better understanding of the Afrotropical lauxaniid fauna. The genus *Minettia* was not previously formally recorded from the Afrotropical Region, but is included in the below identification key, as the genus is now known to occur there. Lauxaniidae are best micro-pinned in the field for later double-mounting (see Chapter 2).

Key to genera of Afrotropical Lauxaniidae

1. Costal wing vein (C) with spinules reaching apex of vein R_{4+5} (e.g., Figs 53, 54), or just short of R_{4+5} (e.g., Fig. 50) (HOMONEURINAE) 2
– Costal wing vein (C) with spinules reaching apex of vein R_{2+3} or slightly beyond (e.g., Fig. 56), or rarely absent (e.g., Fig. 51) (LAUXANIINAE) 7
2. Thorax with downsloping seta near middle of anepisternum (in addition to anepisternal seta at posterior margin), clearly distinguishable from surrounding setulae (Fig. 44); dorsocentral setae 1 + 3 (Fig. 44); with row of distinct acrostichal setae (as in Fig. 29); wing membrane strongly patterned . . . *Trypetisoma* Malloch
– Thorax with only anepisternal seta at posterior margin and setulae (e.g., Fig. 47); dorsocentral setae, acrostichal setae and wing membrane variable. 3
3. Wing narrowing basally without anal lobe (Fig. 54); head with posterior fronto-orbital seta inserted far forwards on frons, with anterior seta minute, very close to posterior seta (as in Fig. 19) . . . . . *Katalauxania* Hendel
– Wing not narrowing basally with distinct anal lobe (e.g., Figs 50, 53); head with posterior fronto-orbital seta inserted on posterior ½ of frons, with anterior seta usually closer to lunule (e.g., Fig. 31). 4
4. Head projecting forward, with frons meeting lunule at acute angle (Fig. 12); face with facial carina as sharp protruding keel in upper ½ (Fig. 13); wing membrane strongly patterned, with costal spinules extending to point just short of vein R_{4+5} (Fig. 50). . . . . .*Cainohomoneura* Stuckenberg
– Head not projecting forward, with frons sloping into lunule (e.g., Figs 15, 16, 45); face without keel; wing variable, but costal spinules fully extended to vein R_{4+5} (e.g., Fig. 53). 5
5. Head with face consisting of broad, silvery pruinose swelling that projects ventrally as lobe over clypeus (Fig. 45); wing membrane hyaline, without markings . . . . . *Zanjensiella* Stuckenberg
– Head with face normal, flat to convex, but not projecting ventrally; wing membrane variable 6
6. Head distinctly higher than long (Fig. 15); gena and subgena high, more than ½ height of eye (Fig. 16); face broad, high, usually with distinct convexity (Fig. 16); frons sometimes with distinct ornamentation, including black velvety pruinose maculae and glossy black maculae (Fig. 16) . . . . . *Cestrotus* Loew
– Head not distinctly higher than long; subgena small, with gena and subgena never higher than ½ height of eye; face variable, but usually lacking convexity; frons lacking distinct velvety pruinose and glossy black ornamentation (Fig. 31) . . . . . *Homoneura* Wulp

7. Wing narrowing basally, without anal lobe (Fig. 55); head with posterior fronto-orbital seta inserted far forwards on frons, with anterior seta minute, very close to posterior seta (Fig. 19); with large velvety black macula covering frons, from postocellar setae through to anterior ½, encompassing entire ocellar triangle (Fig. 19); ocelli far apart, with anterior ocellus far forward to *ca* mid length of frons; dorsocentral setae 0 + 2 . . . . . *Neogeomyza* Séguy

– Wing normal, with distinct anal lobe (e.g., Fig. 56); head with insertion of fronto-orbital setae variable; without velvety black macula from postocellar setae over most of frons; ocelli closely approximated, with anterior ocellus above mid length of frons; dorsocentral setae variable 8

8. Head with face prominently convex, glossy, with paired dark maculae (Figs 20, 36); antenna elongate, with scape up to 2 × longer than pedicel; postpedicel longer than scape and pedicel combined (Fig. 20); anterior fronto-orbital seta inclinate (Fig. 20); ocellar setae minute (Fig. 20) . . . . *Pachycerina* Macquart

– Head with face usually flat or recessed, but if convex, then never glossy with paired dark maculae; antenna variable, but scape never longer than pedicel; anterior fronto-orbital seta and ocellar setae variable 9

9. Thorax without posthumeral seta (Fig. 28); dorsocentral setae 0 + 3 (Fig. 28); head elongated, longer than high; anterior part of frons densely clothed in proclinate setulae (Fig. 28); anterior fronto-orbital seta inclinate (Fig. 28); ocellar and postocellar setae minute (TRIGONOMETOPINI). . . . . *Diplochasma* Knab (*Sauteromyia* Malloch)

– Thorax with posthumeral seta (e.g., Fig. 30); other characters variable 10

10. Thorax with intra-alar seta (e.g., Figs 26, 34, 35). 11

– Thorax without intra-alar seta (e.g., Figs 37, 39, 42, 46–48) 14

11. Head with anterior fronto-orbital seta inclinate (Fig. 22). . . . . *Prosamyza* Stuckenberg

– Head with anterior fronto-orbital seta reclinate (e.g., Figs 23–25) 12

12. Thorax with 1 intra-alar seta on each side (Fig. 34); anepisternum with 1 seta at posterior margin; presutural dorsocentral seta present or absent. . . . . [*Minettia* Robineau-Desvoidy]

– Thorax with 2 intra-alar setae on each side (e.g., Figs 26, 35); anepisternum with 2 setae at posterior margin (e.g., Figs 26, 35); presutural dorsocentral seta absent (e.g., Figs 26, 35) 13

13. Head with ocellar setae weak, short (Fig. 26); thorax with postpronotum with 1–2 smaller setae in addition to strong postpronotal seta (Fig. 26); all tibiae with preapical dorsal seta . . . . . *Afrominettia* Stuckenberg

– Head with ocellar setae strong, subequal to posterior fronto-orbital seta (Fig. 35); thorax with 1 postpronotal seta (Fig. 35); hind tibia without preapical dorsal seta. . . . . *Nimettia* Stuckenberg

14. Wing membrane with strongly reticulated pattern (Fig. 51); costal vein (C) without spinules (Fig. 51); head with ocelli on small, but distinct, tubercle (Fig. 29); scutellum concave anteromedially (Fig. 29); all setae and setulae long and erect (Fig. 29), particularly evident on mesonotum, scutellum and legs . . . . . *Drepanephora* Loew

– Wing membrane variable in pattern, but invariably costal vein (C) with spinules (e.g., Figs 52, 56); head with ocelli never on distinct tubercle, but may be slightly raised (e.g., Figs 17, 25); scutellum flat or arched; setae and setulae variable, but never distinctly long and erect 15

15. Wing with 1–2 auxiliary veins along apical section of vein M_1, projecting into cell m_1 (e.g., Fig. 52). . . 16

– Wing without auxiliary veins along vein M_1 (e.g., Fig. 56) 17

16. Wing with 2 auxiliary veins along vein M_1 (Fig. 52); thorax without presutural dorsocentral seta (Fig. 30); head with frons extending only slightly beyond eye (Fig. 17); face at right or obtuse (Fig. 17) angle from frons; eye elongate in oblique-vertical orientation (Fig. 17); lacking fascia between anterior eye margin and upper parafacial (Fig. 17) . . . . . *Dyticomyia* Stuckenberg

– Wing with 1 auxiliary vein along vein M_1; thorax with presutural dorsocentral seta; head with frons projecting forward well beyond eye; face receding at acute angle from frons; eye elongate in horizontal orientation; with brown to black fascia between anterior eye margin and upper parafacial. . . . . *Proteaphila* Davies & Miller

17. Head with face strongly convex (e.g., Fig. 25), or bulging in upper ½, due to transverse depression (e.g., Figs 14, 18), usually glossy (Fig. 14), but sometimes with faint whitish pruinosity; fronto-orbital plates usually glossy (e.g., Fig. 18) 18

– Head with face flat or concave, usually dull; fronto-orbital plates not glossy 20

18. Head without ocellar setae (Fig. 25); body yellowish to yellowish brown; frons uniformly flattened or arched (Fig. 25); face evenly convex (Fig. 25). . . . . *Xangelina* Walker

– Head with ocellar setae (e.g., Figs 14, 18); body black or partly black or metallic (e.g., Figs 14, 18, 33); anterior part of frons turned up (e.g., Figs 14, 18); face bulging in upper ½, usually separated from lower ½ by transverse depression (e.g., Figs 14, 18) 19

19. Antenna short, scape recessed (Fig. 14); postpedicel < 2 × longer than scape and pedicel combined (Fig. 14) . . . . . *Calliopum* Strand

– Antenna elongated, with scape long and fully exposed (Figs 18, 33); postpedicel 2 × or more longer than scape and pedicel combined, several times longer than high (Figs 18, 33). . . . . *Lauxania* Latreille

20. Thorax without presutural dorsocentral seta (e.g., Figs 38, 39, 42, 49) 21

– Thorax with presutural dorsocentral seta (e.g., Figs 37, 40, 43, 46–48) 24

21. Head with posterior fronto-orbital seta usually inserted far forward on frons, with smaller anterior seta closely approximated (Figs 38, 39); antennal arista plumose (Figs 38, 39) . . . *Parapachycerina* Stuckenberg

– Head with posterior fronto-orbital seta inserted on posterior ½ of frons (e.g., Figs 23, 24, 42, 49); antennal arista pubescent (e.g., Figs 23, 24, 42, 49) 22

22. Head not higher than long (Figs 23, 24, 42); frons flat or arched (Figs 23, 24, 42); anterior fronto-orbital seta in anterior ½ of frons, posterior seta in posterior ½ (Figs 23, 24, 42); antennae closely approximated (Figs 23, 24, 42) . . . . . *Sapromyza* Fallén

– Head distinctly higher than long (Fig. 49); frons concave or with transverse depression (e.g., Fig. 49); fronto-orbital setae both in posterior ½ of frons, with anterior seta located at mid length of frons (e.g., Fig. 49); antennae widely separated, by more than width of antennal base (e.g., Fig. 49) 23

23. Head not appearing thickened, gena small, with height < ½ height of eye; both fronto-orbital setae small; wing with flexure line to hold over abdomen in flexed position, with vein R_{2+3} curved towards, and closely associated with, costal vein (C) . . . . . *Teratolauxania* Stuckenberg

– Head appearing thickened, with broad gena, nearly ½ height of eye (Fig. 49); anterior fronto-orbital seta ½ size of normal-sized posterior fronto-orbital seta (Fig. 49); wing without flexure line, with vein R_{2+3} running almost parallel with, and not curved towards, costal vein (C) . . . . . Undescribed genus D

24. Thorax with dorsocentral setae arrangement 1 + 2 (e.g., Figs 37, 40, 47) 25

– Thorax with dorsocentral setae arrangement 1 + 3 (e.g., Figs 46, 48) 27

25. Head with anterior fronto-orbital seta reclinate (Fig. 47); ocellar setae strong (Fig. 47); head and eye higher than long (Fig. 47) . . . . . Undescribed genus B

– Head with anterior fronto-orbital seta inclinate (e.g., Fig. 37), at least at tips (e.g., Fig. 21); ocellar seta weak (e.g., Figs 21, 37); head usually longer than high (e.g., Fig. 40) or subequal, but if slightly higher than long, then gena large, nearly same height as eye (e.g., Fig. 37) 26

26. Head with facial setae along oral margin not enlarged (Fig. 37); without orbito-antennal macula (Fig. 37). . . . . *Panurgopsis* Kertész

– Head with facial setae along oral margin enlarged (Figs 21, 40); with orbito-antennal macula (Fig. 21) . . . . . *Prochaetops* Bezzi

27. Antennal postpedicel rounded distally (Fig. 46); clypeus not enlarged; anterior fronto-orbital seta set back from anterior margin of frons (Fig. 46); frons arched, evenly sloping into face, with face not receding. . . . . Undescribed genus A

– Antennal postpedicel subtriangular, broad basally, converging to tip (e.g., Figs 43, 48); clypeus enlarged, protruding (e.g., Figs 43, 48); anterior fronto-orbital seta inserted at anterior margin of frons (e.g., Figs 43, 48); frons flat or slightly concave, with face receding at angle to frons (e.g., Figs 43, 48) 28

28. Body conspicuously maculate (Fig. 43); anterior frons bare; anterior fronto-orbital seta reclinate (Fig. 43); antennal arista subbasal, with short even pubescence (Fig. 43) . . . . . *Spathecerus* Lindner

– Body largely orange, with thorax brown dorsally (Fig. 48); anterior frons setulose (Fig. 48); anterior fronto-orbital seta inclinate (Fig. 48); antennal arista subapical, with basal-most microtrichia longest, with ventrobasal cluster of long microtrichia (Fig. 48) . . . . . Undescribed genus C

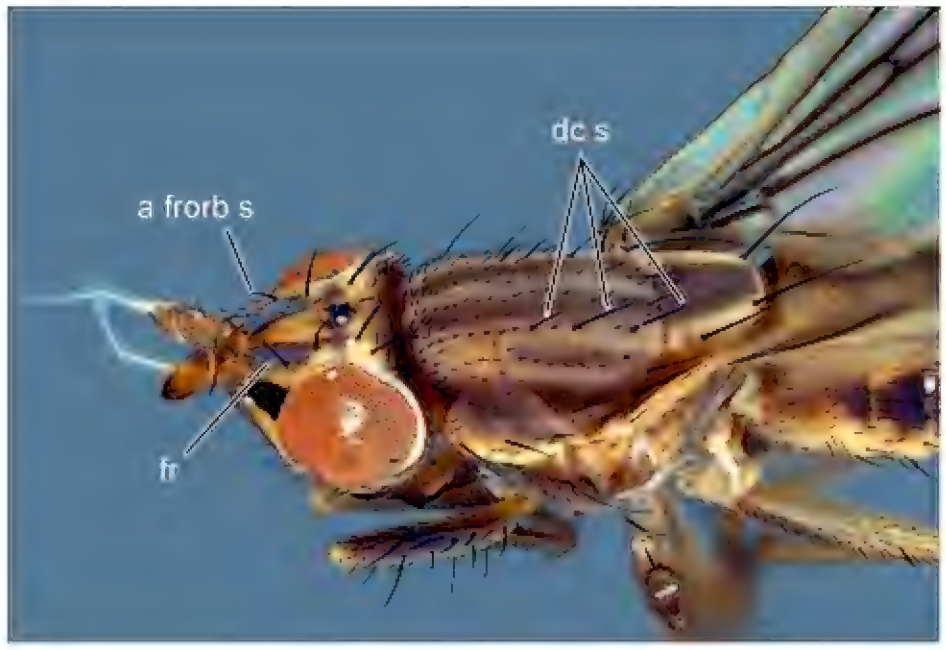
Synopsis of the fauna

Lauxaniidae are extremely diverse worldwide, with their greatest diversity in both the Old and New World tropics (Stuckenberg 1971). Three genera are virtually cosmopolitan, *Homoneura*, *Minettia* and *Sapromyza*, each of which, after substantial revisionary work, will likely be found to represent several distinct lineages. This has already occurred for the non-Afrotropical genus *Trigonometopus* Macquart, previously thought to be more widespread. Of these genera, it

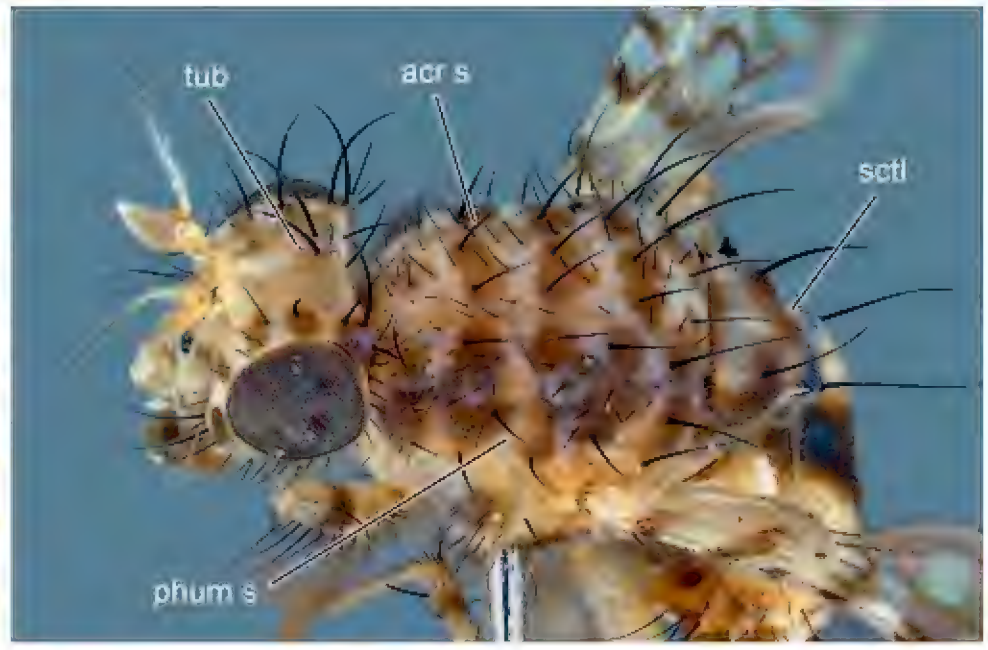
is interesting to note that the Neotropical fauna contains no species of *Homoneura*, and in fact, no species of the subfamily Homoneurinae, except for two species of *Trypetisoma*, a genus that also occurs in the Afrotropics and may or may not be a homoneurine.

Of the 25 total Afrotropical genera and subgenera, 11 are endemic to the region, eight of which are monotypic. Of the six genera occurring on Madagascar, two (*Nimettia* and *Zanjensiella*) appear to be endemic, with three species total. Although no other genera are Afrotropical island endemics, there are 26 species in six genera (*Diplochasma*, *Homoneura*, *Neogeomyza*, *Pachycerina*, *Parapachycerina* and *Trypetisoma*) that are island endemics, with eight more in Madagascar, 10 in Seychelles, seven on the Mascarene Is., and one on the Atlantic Ocean island of São Tomé. Of the non-endemic genera, most have congeners in the Palaearctic or Oriental Regions, with a few being still more widespread. In total, the described Afrotropical fauna is small, consisting of 114 species. It is readily apparent after study that only a small fraction of the fauna is known, with likely hundreds of new species yet to be described. The immature stages are unknown for any Afrotropical species, and besides the genera *Pachycerina* and *Proteaphila*, the same can be said for biological activities. Furthermore, except where noted, no identification keys to Afrotropical species are currently available.

Afrominettia Stuckenberg (Lauxaniinae)**.** An endemic monotypic genus, with the single described species, *A. jeanneli* (Séguy, 1938), described from Cameroon and Kenya. Like other



28 *Diplochasma* (*Sauteromyia*) ♀



29 *Drepanephora* ♀

30 *Dyticomyia* ♂

31 *Homoneura* ♂

Figs 74.28–31. Heads and thoraces, thorax and habitus of Lauxaniidae: (28) head and thorax of *Diplochasma* (*Sauteromyia*) *variegata* Papp, dorsolateral view ♀; (29) same, *Drepanephora africana* (Curran), dorsolateral view ♀; (30) thorax of *Dyticomyia oraria* Stuckenberg, lateral view ♂; (31) habitus of *Homoneura* sp., dorsolateral view ♂.

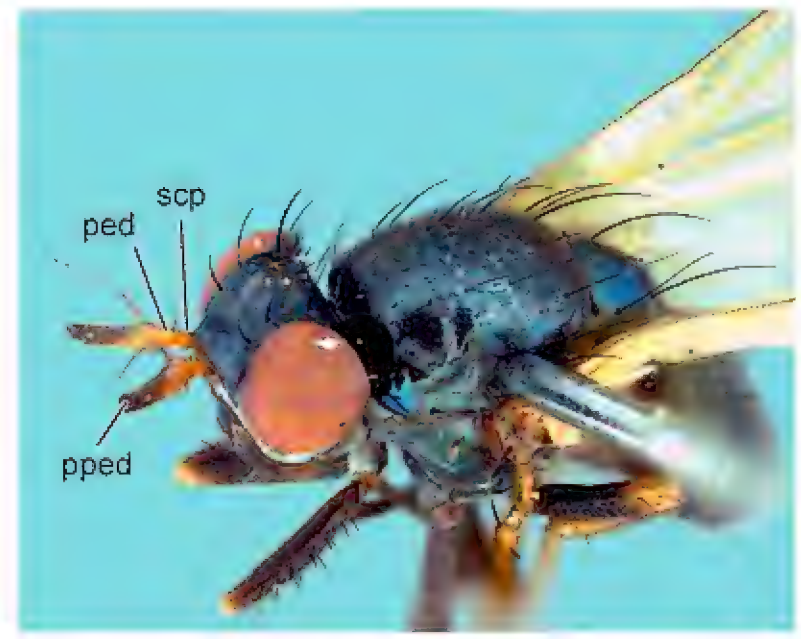
Abbreviations: a frorb s – anterior fronto-orbital seta; acr s – acrostichal seta; dc s – dorsocentral setae; fr – frons; p frorb s – posterior fronto-orbital seta; phum s – posthumeral seta; sctl – scutellum; tub – tubercle.

genera related to *Minettia*, the genus has an intra-alar seta, and like *Nimettia*, there are two intra-alar setae on each side, the anepisternum has two setae on the posterior margin and there is no presutural dorsocentral seta. The genus is further characterised by short and weak ocellar setae, one or two smaller setae on the postpronotum, besides the strong postpronotal seta and all tibiae have a preapical dorsal seta.

Cainohomoneura Stuckenberg (Homoneurinae)**.** An endemic monotypic genus, with the single described species, *C. delta* Stuckenberg, 1971, described from South Africa. This species is found only in the coastal scarp forests of the KwaZulu-Natal Province. Like other homoneurine genera, the genus has the costal spinules extending to wing vein R_{4+5}, but the spinules terminate just short. The genus is characterised by a forward-projecting head, with the frons meeting the lunule at an acute angle, the presence of a sharp protruding keel in the upper part of the face between the antennae and the wing membrane being strongly patterned.

Calliopum Strand (Lauxaniinae)**.** A genus of 28 described species, mainly occurring in the Afrotropical and Palaearctic Regions (but with five species in the Nearctic), including North Africa and from Portugal through China. The genus includes only two described species in the Afrotropics: *C. indecorum* (Loew, 1862) occurring in Southern Africa (*i.e.*, South Africa and bordering countries) and *C. rufipes* (Czerny, 1932) from Yemen. Undescribed species are known from throughout the Afrotropics, including Madagascar, although some species that sort here may be congeneric with those species that sort to *Lauxania*. In South Africa, specimens are known from various habitat types, such as Fynbos and other scrublands and from indigenous montane and *Ficus*-dominated forests. Pérusse & Wheeler (2000) suggested that the affinities between this genus and *Lauxania* are yet to be worked out. Both genera share being black or nearly black and having a glossy, convex (at least in the upper half) face and glossy fronto-orbital plates. In this work the genus is separated from *Lauxania* on the basis of the antennae being short, with a recessed scape. It should

32 *Homoneura* ♀



33 *Lauxania* ♀

34 *Minettia* ♀

35 *Nimettia* ♀

Figs 74.32–35. Heads and thoraces and habitus of Lauxaniidae: (32) habitus of *Homoneura* sp., dorsolateral view ♀; (33) head and thorax of *Lauxania* sp., dorsolateral view ♀; (34) same, *Minettia* sp., dorsolateral view ♀; (35) same, *Nimettia biseta* Stuckenberg, dorsolateral view ♀.

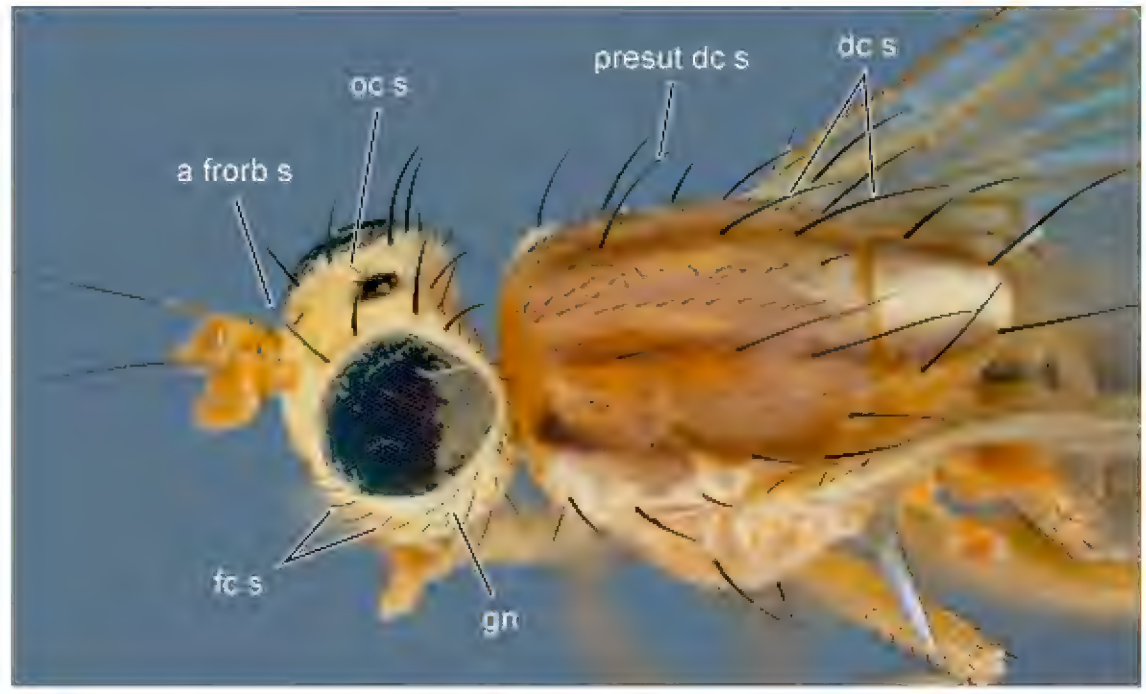
Abbreviations: anepst s – anepisternal setae; ial s – intra-alar seta(e); oc s – ocellar seta; ped – pedicel; pped – postpedicel; pprn s – postpronotal seta; scp – scape.

be noted that the undescribed species that sort here are often only very slightly different from *Lauxania*.

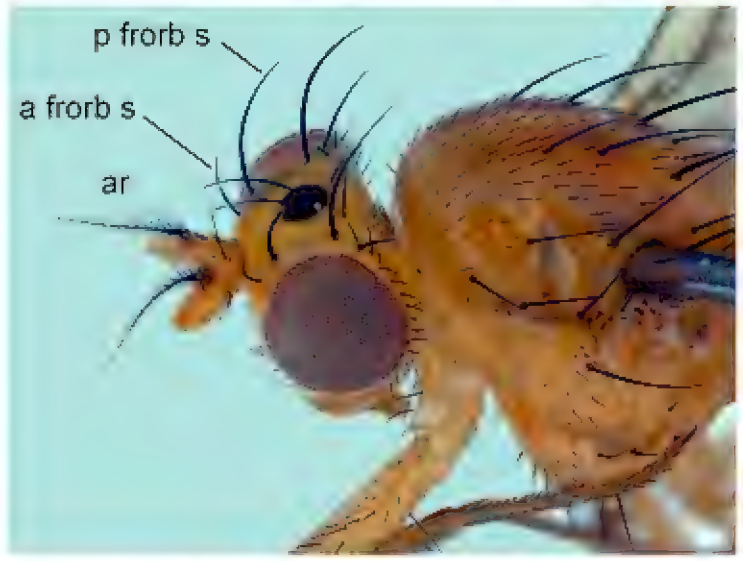
Cestrotus Loew (Homoneurinae)**.** A genus of 25 described species occurring in the Afrotropical and Oriental Regions. One of the dominant lauxaniid genera in the Afrotropics, with 13 described species and many undescribed, occurring in various habitats from wet to dry forests, scrublands and savanna. The genus is also species rich in the Oriental Region, with another 12 described species and numerous undescribed. The most widespread species appear to be *C. megacephalus* Loew, 1862 and *C. variegatus* Loew, 1862, known from Central and Southern Africa. Although there are no described species from Madagascar, the genus does occur there and is commonly encountered. Like the other homoneurine genera, this genus has the costal spinules extending all the way to wing vein R_{4+5}. The genus is otherwise characterised by the head being distinctly higher than long, also with a high gena and subgena of greater height than half the eye height, the face is broad and high, usually with a distinct convexity, the frons is sometimes ornamented with black velvety pruinose and/or glossy maculae and the wing membrane is often distinctly patterned. A partial identification key to eight of the 13 Afrotropical species was provided by Lindner (1956).

Diplochasma Knab (Lauxaniinae: Trigonometopini)**.** A genus of 12 described species occurring in the Afrotropical, Australasian and Oriental Regions. In the Afrotropics the genus is only represented by eight species of the subgenus *D.* (*Sauteromyia* Malloch), which is also the sole representative of the tribe Trigonometopini that occurs in the region (Papp 2007, 2008). The genus is considerably more widespread through Asia, South-east Asia and into Australia, although this subgenus does not appear to occur in Australia. For sub-Saharan Africa, Papp (2008) described all eight Afrotropical species of the subgenus, with two rather widespread species: *D.* (*S.*) *albomarginata* Papp, 2008, occurring in West, Central and Southern Africa and *D.* (*S.*) *variegata* Papp, 2008, in Central and Southern Africa. One species, *D.* (*S.*) *stuckenbergi* Papp, 2008, is endemic to Madagascar and the remaining species are more

36 *Pachycerina* ♂



37 *Panurgopsis* ♀



38 *Parapachycerina* ♂

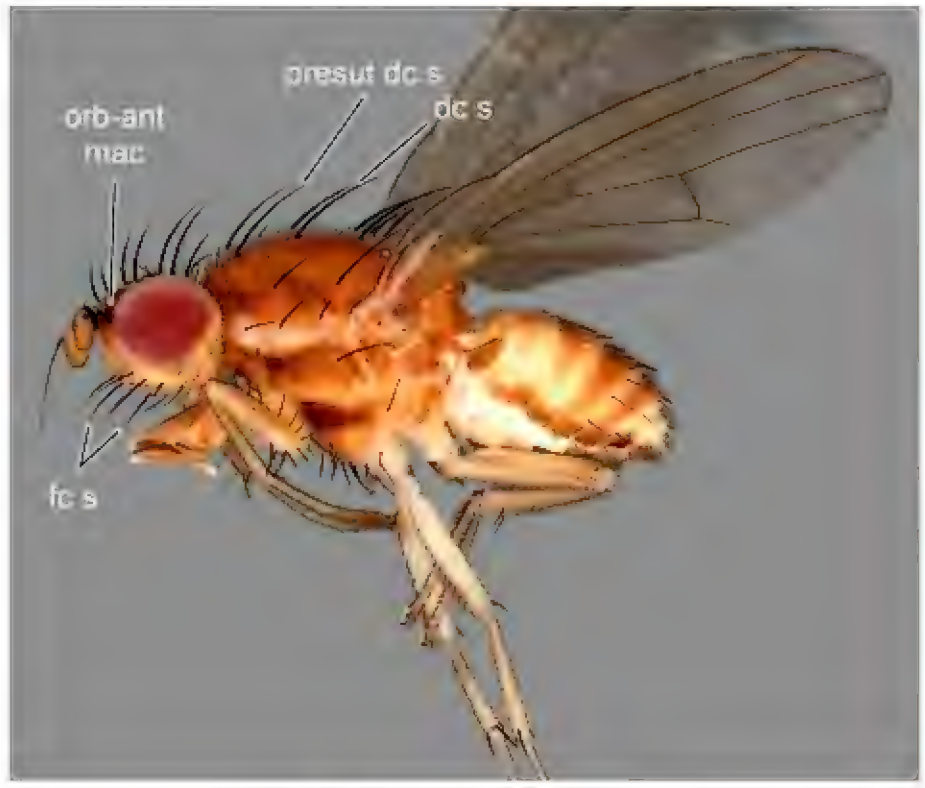
39 *Parapachycerina* ♀

Figs 74.36–39. Habitus and heads and thoraces of Lauxaniidae: (36) habitus of *Pachycerina* sp., lateral view ♂; (37) head and thorax of *Panurgopsis* sp., dorsolateral view ♀; (38) same, *Parapachycerina bispina* Davies & Miller ♂; (39) same, *Parapachycerina* sp. ♀.

Abbreviations: a frorb s – anterior fronto-orbital seta; ar – arista; dc s – dorsocentral setae; fc s – facial setae; gn – gena; oc s – ocellar seta; p frorb s – posterior fronto-orbital seta; presut dc s – presutural dorsocentral seta.

restricted, but mostly occur in Central and Southern Africa, with one species in Ghana. The subgenus is characterised by the absence of a posthumeral seta, the head being elongated with the anterior part of the frons densely clothed in proclinate setulae, the anterior fronto-orbital seta is inclinate, the ocellar and postocellar setae being minute, the anterior part of the gena and oral margin have enlarged setae in a row and the dorsocentral setae conformation is 0 + 3. An identification key to the eight Afrotropical species was provided by Papp (2008).

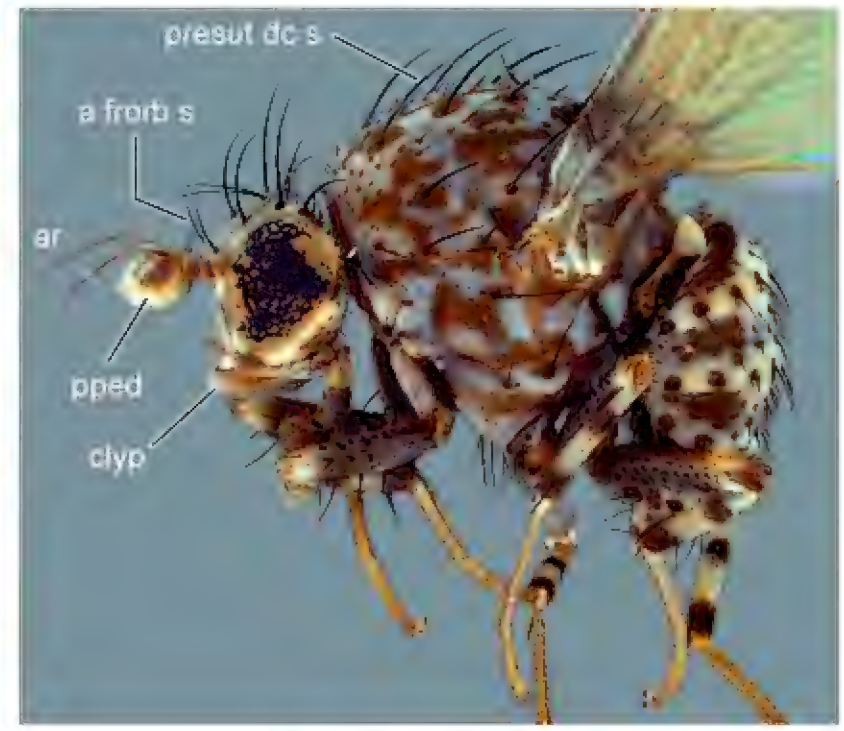
Drepanephora Loew (Lauxaniinae)**.** A genus of eight described species occurring in the Afrotropical and Oriental Regions. Three species are Afrotropical, the rest are known from India and Sri Lanka to South-east Asia. *Drepanephora africana* (Curran, 1938) was described from West Africa, but appears to be rather widespread, while the other two species are more restricted in their distributions, with *D. bicalcarata* Speiser, 1924, known from Tanzania and *D. lindneri* Stuckenberg, 1963, from South Africa. Although undescribed species are known, including from Madagascar, representatives of the genus are rarely encountered. The genus is particularly distinct within the family, being characterised by the absence of costal spinules on the wing, the ocelli being placed on a small, but distinct tubercle, the scutellum being concave anteromedially and being covered throughout by long and erect setae and setulae, particularly evident on the mesonotum, scutellum and legs.



40 *Prochaetops* ♀

41 *Prosamyza* ♀

42 *Sapromyza* ♂



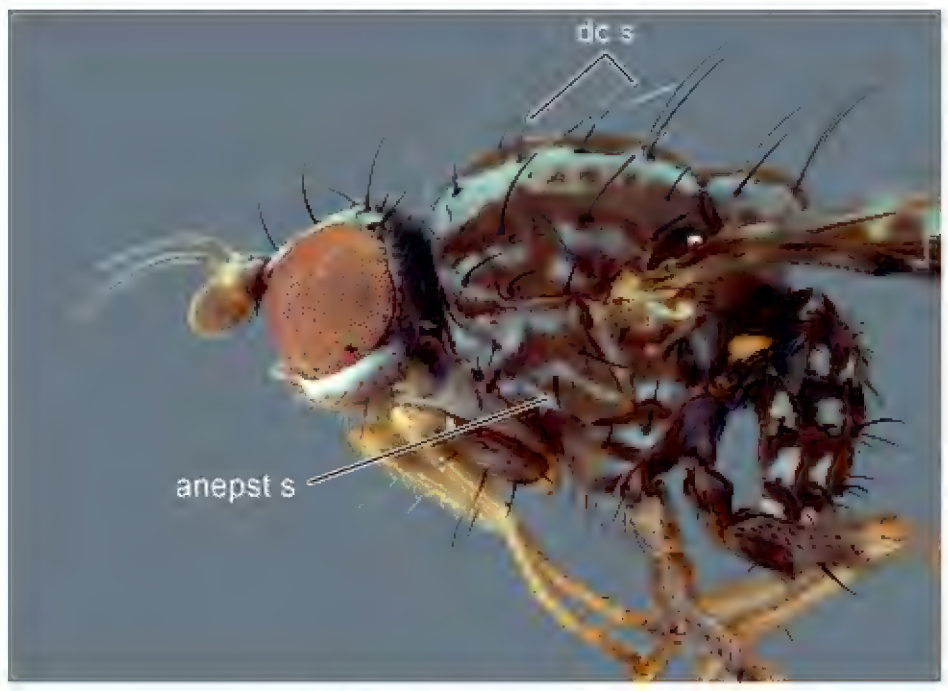
43 *Spathecerus* ♀

Figs 74.40–43. Habitus and heads and thoraces of Lauxaniidae: (40) habitus of *Prochaetops* sp., lateral view ♀; (41) same, *Prosamyza* sp., dorsolateral view ♀; (42) same, *Sapromyza* sp. ♂; (43) same, *Spathecerus multipunctatus* Lindner, lateral view ♀.

Abbreviations: a frorb s – anterior fronto-orbital seta; ar – arista; clyp – clypeus; dc s – dorsocentral seta; fc s – facial setae; fr – frons; orb-ant mac – orbital-antennal macula; p frorb s – posterior fronto-orbital seta; pped – postpedicel; presut dc s – presutural dorsocentral seta.

Dyticomyia Stuckenberg (Lauxaniinae)**.** An endemic monotypic genus, with the single described species, *D. oraria* Stuckenberg, 1971, described from South Africa. Although not the only Afrotropical genus with an auxiliary vein along wing vein M_1 projecting into cell m_1 (*Proteaphila* being the other), this is the only genus with two such auxiliary veins. The genus is also characterised by lacking a presutural dorsocentral seta, having the face oriented at a right or obtuse angle from the frons and a vertically elongated eye.

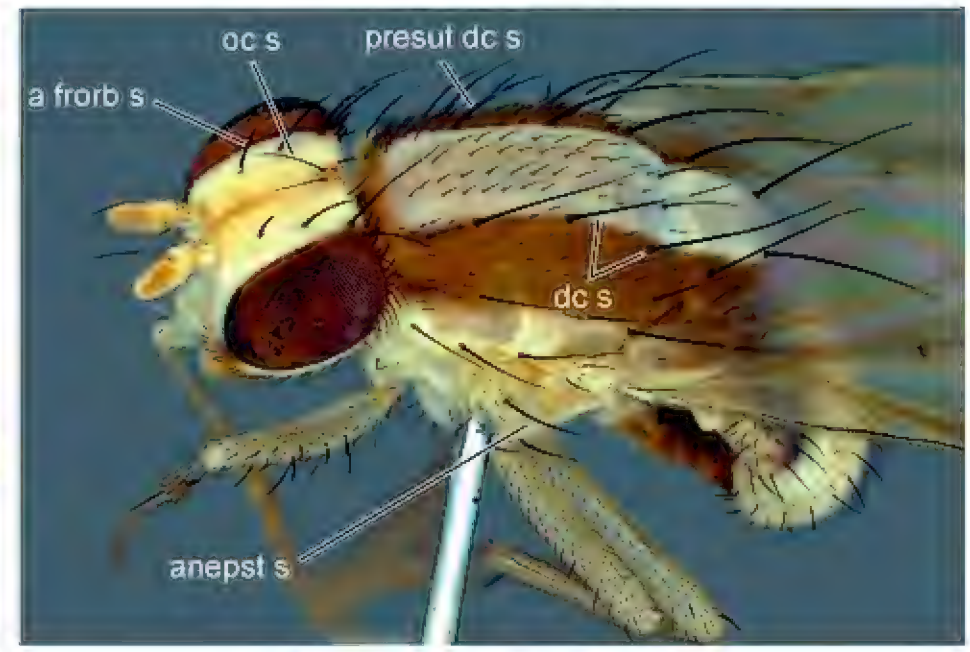
Homoneura Wulp (Homoneurinae)**.** A virtually cosmopolitan genus of > 600 described species, occurring in all zoogeographical regions, except the Neotropical Region and Antarctica. *Homoneura* is the most diverse lauxaniid genus in the Afrotropics, with 30 described species occurring throughout the region, including the Indian Ocean islands of Seychelles (7 species) and the Mascarenes Is. (6 species). Unlike *Lauxania*, *Meiosimyza* (*Lyciella*) and *Sapromyza*, these species belong to what is considered the "true" *Homoneura*, which is the most diverse genus within the family. Although *Homoneura* requires much revisionary work, it is not considered a "dumping-ground" for difficult to place species, although its division into monophyletic subgenera is a great difficulty at this time and all Afrotropical species are considered to belong to the subgenus *Homoneura sensu stricto*. Numerous undescribed species are known from throughout the Afrotropics, including extreme diversity in Madagascar. Like the other homoneurine genera, the genus has the costal spinules extending all the way to wing vein R_{4+5}. Among homoneurines, the genus can be distinguished by the combination of a single anepisternal seta at the posterior margin of the anepisternum, the wing with a distinct anal lobe, the frons sloping evenly into the lunule, the anterior fronto-orbital seta being closer to the lunule than to the posterior seta, the face being flattened and lacking a central keel and the frons lacking pruinose or glossy ornamentation. This genus is in need of revision for the Afrotropical fauna, with the most recent identification key to the Afrotropical species provided by Curran (1938), including only 14 species and noting that



44 *Trypetisoma* ♀

45 *Zanjensiella* ♂

46 Undescribed genus A ♀



47 Undescribed genus B ♀

Figs 74.44–47. Heads and thoraces of Lauxaniidae: (44) *Trypetisoma* sp., lateral view ♀; (45) same, *Zanjensiella argentifrons* Stuckenberg ♂; (46) Undescribed genus A, dorsolateral view ♀; (47) same, Undescribed genus B ♀.

Abbreviations: a frorb s – anterior fronto-orbital seta; anepst s – anepisternal seta; dc s – dorsocentral setae; fc lb – facial lobe; oc s – ocellar seta; pped – postpedicel; presut dc s – presutural dorsocentral seta.

most of the species he listed (without an identification key) in *Sapromyza* likely belong here.

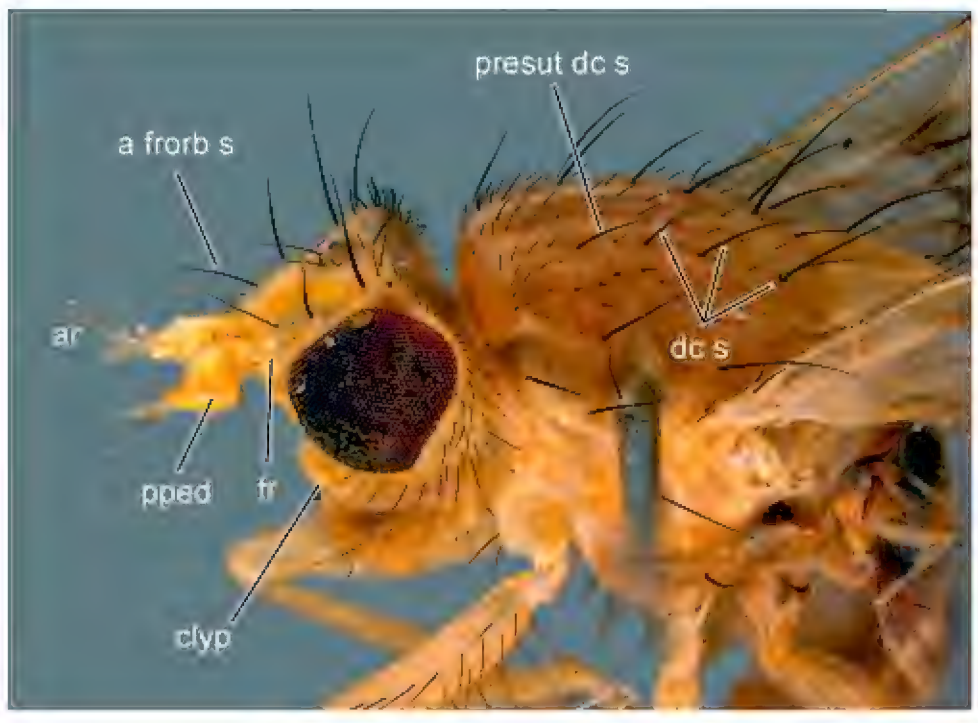
Katalauxania Hendel (Homoneurinae)**.** An endemic monotypic genus, with the single described species, *K. variipennis* Hendel, 1925, described from Tanzania. Like the other homoneurine genera, the genus has the costal spinules extending all the way to wing vein R_{4+5}. The genus is characterised by the absence of an anal lobe on the basally narrowed wing and the composition of the fronto-orbital setae, with the posterior seta inserted far forwards on the frons and the anterior seta being minute and inserted very close to the posterior seta.

Lauxania Latreille (Lauxaniinae)**.** A genus of 30 described species occurring in the Afrotropical, Nearctic, Neotropical and Palaearctic Regions. Nine described species occur in the Afrotropics, representing nearly one-third of the known diversity of this otherwise mainly Holarctic genus. Pérusse & Wheeler (2000) suggested that the genus is restricted to the Holarctic, which would leave the Afrotropical species as having unknown generic affiliations. Like *Sapromyza*, it is possible that the Afrotropical fauna has few, if any true representatives of the genus, yet many specimens are sorted under this name. Numerous undescribed species are known from the region, including Madagascar, but it is possible that they represent a different genus or genera (and some may be congeneric with species that currently sort to *Calliopum*). This fact and the several currently valid species in this genus from the Afrotropics, are a reflection of the need to define their true affinities. Pérusse & Wheeler (2000) suggested that the affinities between this genus and *Calliopum* are yet to be defined. Both genera share being black or nearly black and having a glossy, convex (at least in the upper half) face and glossy fronto-orbital plates. In this work, the genus is separated from *Calliopum* on the basis of the antennae being greatly elongated, including elongation of the scape and pedicel. It should be noted that the undescribed species that sort here are often only scarcely different from *Calliopum*. An identification key to eight Afrotropical species, at least one of which belongs to *Calliopum* (*i.e.*, *C. indecorum*), was provided by Curran (1938), noting that this genus, and *Calliopum*, are in great need of revision.

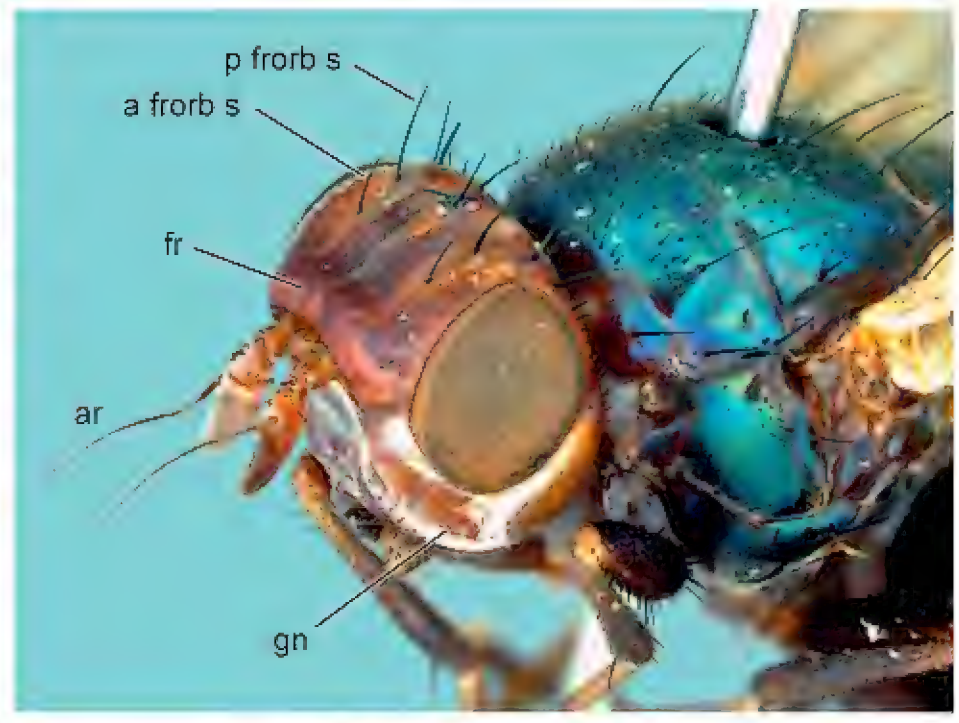
[***Minettia*** Robineau-Desvoidy (Lauxaniinae)**.** A virtually cosmopolitan genus of more than 100 described species, occurring in all zoogeographical regions, except Antarctica. There are currently no described Afrotropical species. As is the case in most regions, there are likely many new species of this genus in the Afrotropics, at least some of which are known from Central Africa. Some features of this genus are common throughout the family, such as the flat or recessed face, both fronto-orbital setae being reclinate and the presence of a posthumeral seta, but the genus can be separated from others based on the presence of a single intra-alar seta and the single anepisternal seta on the posterior margin. Three other genera have intra-alar setae. The first, *Prosamyza*, differs from *Minettia* in having the anterior fronto-orbital seta inclinate. The others, *Afrominettia* and *Nimettia*, both have two intra-alar setae on each side and two anepisternal setae along the posterior margin.]

Neogeomyza Séguy (Lauxaniinae)**.** A rarely encountered endemic genus of two described species: *N. antennata* Séguy, 1938, described from Kenya and *N. stenoptera* (Stuckenberg, 1971), confined to Madagascar. Representatives of the genus are very small-bodied and delicate flies, with a dorsocentral setae arrangement of 0 + 2 and with the wing narrowing basally so the anal lobe is absent. They are otherwise characterised by having a tiny anterior fronto-orbital seta, and both fronto-orbital setae inserted far forwards on the frons and presence of a large velvety black macula encompassing the postocellar setae through most of the frons.

Nimettia Stuckenberg (Lauxaniinae)**.** An endemic monotypic genus, with the single described species, *N. biseta* Stuckenberg,



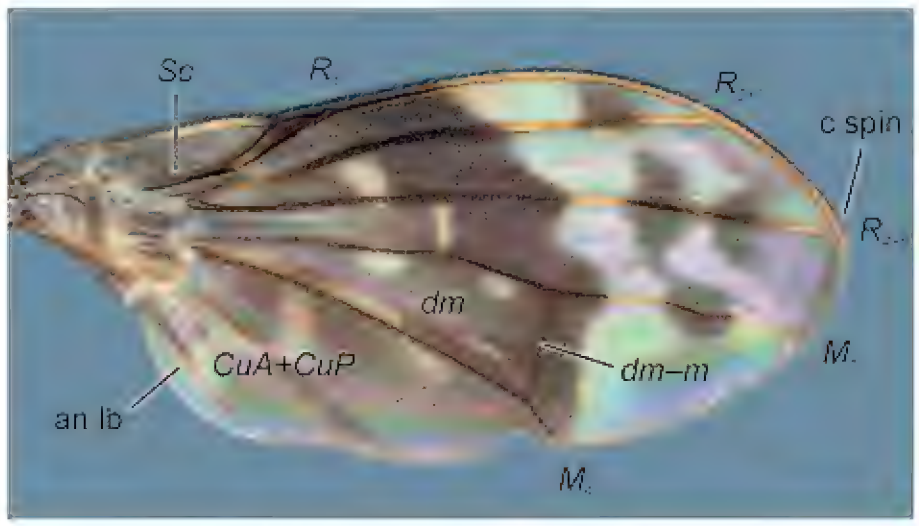
48 Undescribed genus C ♀



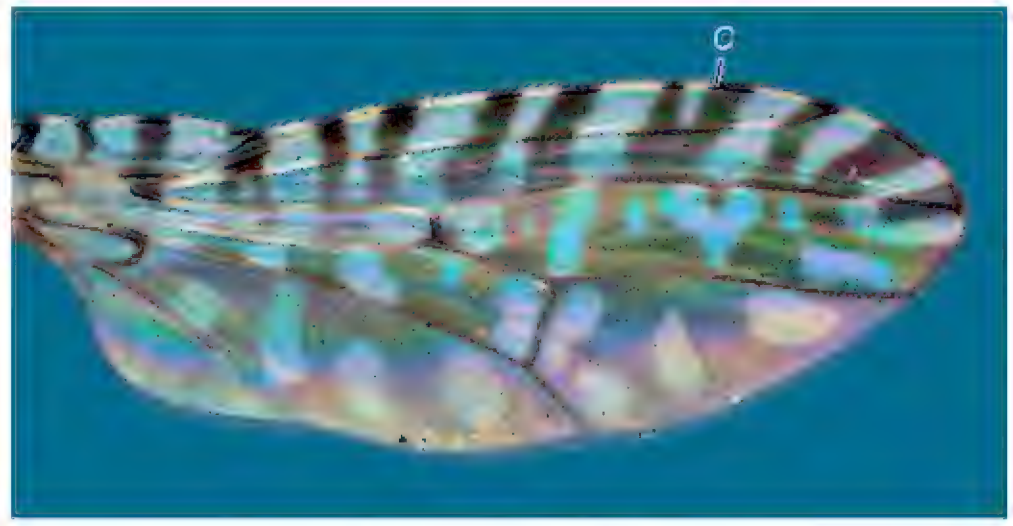
49 Undescribed genus D ♀

Figs 74.48–49. Heads and thoraces of Lauxaniidae: (48) Undescribed genus C, dorsolateral view ♀; (49) Undescribed genus D, anterior oblique view ♀.

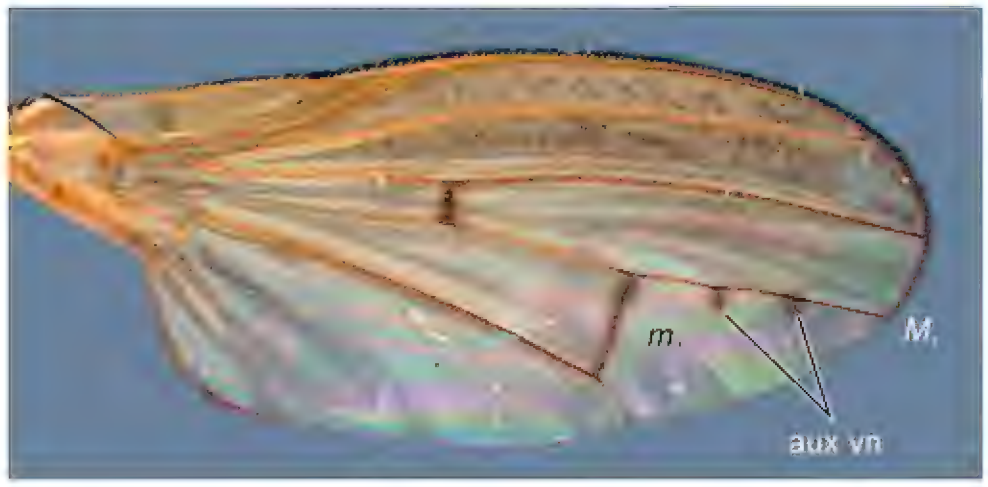
Abbreviations: a frorb s – anterior fronto-orbital seta; ar – arista; clyp – clypeus; dc s – dorsocentral setae; fr – frons; gn – gena; p frorb s – posterior fronto-orbital seta; pped – postpedicel; presut dc s – presutural dorsocentral seta.



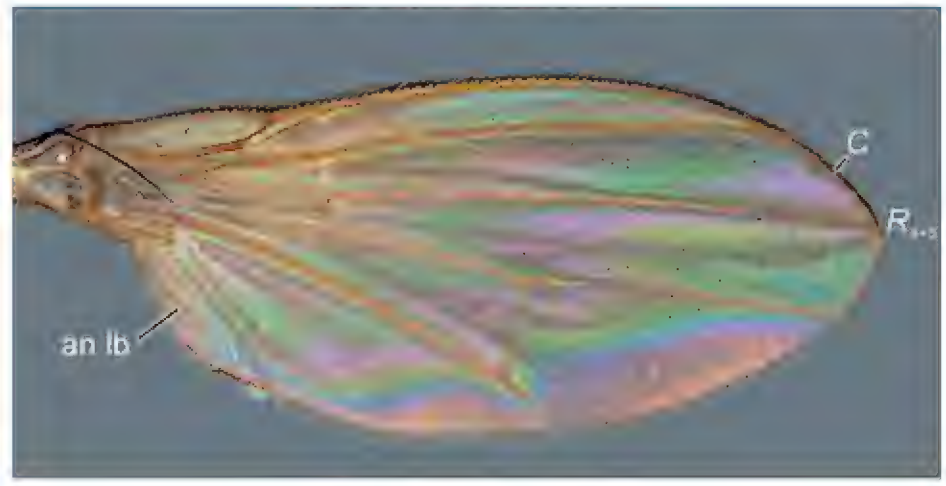
50 *Cainohomoneura* ♀



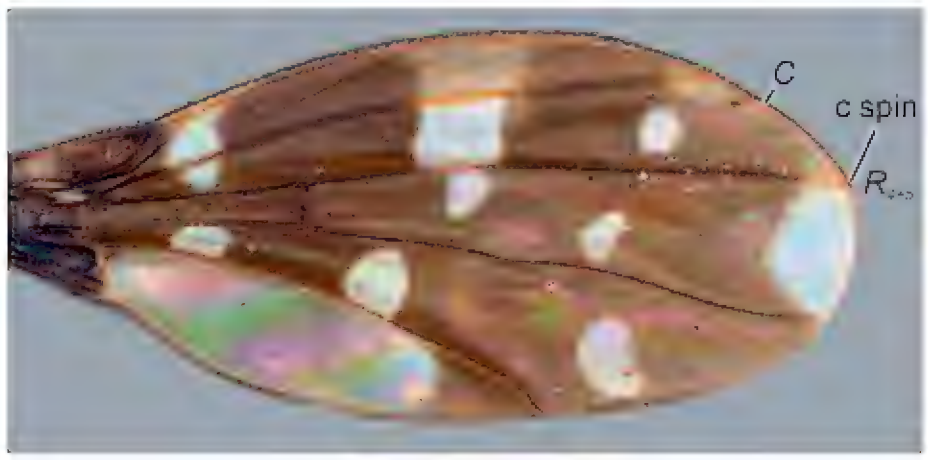
51 *Drepanephora* ♀



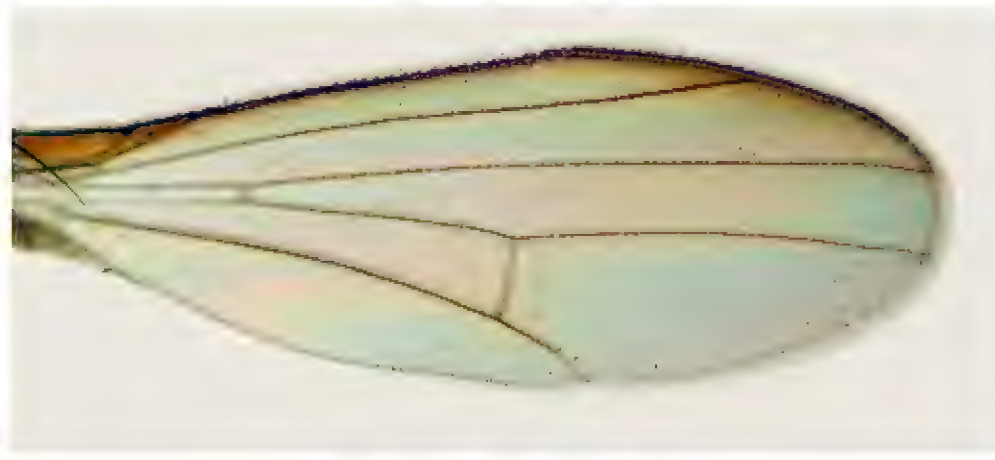
52 *Dyticomyia* ♂



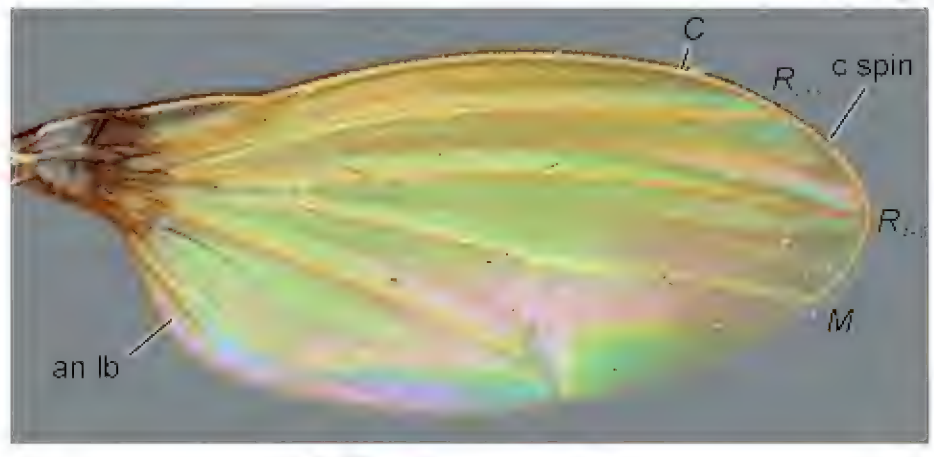
53 *Homoneura* ♀



54 *Katalauxania* ♂



55 *Neogeomyza* ♂



56 *Spathecerus* ♀

Figs 74.50–56. Wings of Lauxaniidae (dorsal views): (50) *Cainohomoneura delta* Stuckenberg ♀; (51) *Drepanephora africana* (Curran) ♀; (52) *Dyticomyia oraria* Stuckenberg ♂; (53) *Homoneura* sp. ♀; (54) *Katalauxania variipennis* Hendel ♂; (55) *Neogeomyza antennata* Séguy ♂; (56) *Spathecerus multipunctatus* Lindner ♀.

Abbreviations: an lb – anal lobe; aux vn – auxiliary vein; *C* – costal vein; c spin – costal spinules; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *dm* – discal medial cell; *dm–m* – discal medial crossvein; M_1 – first branch of media; m_1 – first medial cell; M_4 – fourth branch of media; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *Sc* – subcostal vein.

1971, confined to Madagascar. Like other genera related to *Minettia*, the genus has an intra-alar seta, and like *Afrominettia*, there are two intra-alar setae on each side, the anepisternum has two setae on the posterior margin and there is no presutural dorsocentral seta. This genus is further characterised by the strong ocellar setae, the lack of additional setae on the postpronotum besides the single strong seta and the hind tibia lacks a preapical dorsal seta.

Pachycerina Macquart (Lauxaniinae)**.** A widespread Old World genus of 27 described species, occurring in the Afrotropical, Oriental and Palaearctic Regions. The 11 described Afrotropical species represent more than one-third of the species known globally, but additional species await description. Only three species occur in the continental Afrotropics, all in the southern third of the continent, with one species, *P. vaga* Adams, 1905, extending northwards through Kenya to Eritrea and Ethiopia. The remaining species are restricted to the Indian Ocean islands of Madagascar (4 species), Mauritius (1) and Seychelles (2) and the Atlantic Ocean island of São Tomé (1). Species of the genus are extensively marked, fasciate, maculate and colourful, being distinctive in being predominantly yellow and brown, with distinct longitudinal vittae, a prominently convex glossy face with paired dark maculae, elongate antennae with a particularly long scape and the postpedicel longer than the scape and pedicel combined. They also have an inclinate anterior fronto-orbital seta, minute ocellar setae and only a pair of rows of acrostichal setulae. A particularly unusual state in this genus is the lack of a phallus, membranous or otherwise, which is also a characteristic of Celyphidae (see Chapter 75) and a few genera of lauxaniids. Davies & Miller (2009) included some rearing records for the genus that indicate larvae are likely saprophages in birds' nests and in leaf litter, otherwise nothing is known of their biology and immature stages. Davies & Miller (2009) revised the Afrotropical species and provided an identification key to males (only), although additional undescribed species are likely to occur in the region.

Panurgopsis Kertész (Lauxaniinae)**.** Currently a monotypic genus, with the single described species, *P. flava* Kertész, 1915, being non-Afrotropical and restricted in Asia. There are, however, several undescribed species of the genus which have been recognised from the region, including specimens from Malawi and Uganda. *Panurgopsis* is characterised by being small-sized, lacking a black orbito-antennal macula, the anterior fronto-orbital setae are inclinate, at least at the tips, the ocellar setae are weak and the head is usually longer than high or subequal.

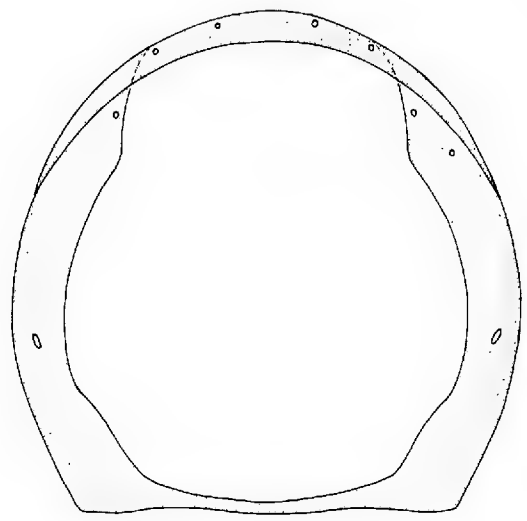
Parapachycerina Stuckenberg (Lauxaniinae)**.** A genus of seven described species occurring in the Afrotropical and Oriental Regions, five of which occur in the Afrotropics and two in East and South-east Asia. Of the described Afrotropical species, two are endemic to Madagascar and the remaining three are widespread in sub-Saharan Africa. Several undescribed species are known that were included (but not described) in the revision of Davies & Miller (2008) and other new species are likely. Species of this genus are usually yellow-orange, being otherwise characterised in having a large dark brown or black ocellar plate, with strong proclinate ocellar setae, fronto-orbital setae inserted far forward on the frons and very closely approximated, with the posterior seta very long and the anterior seta diminutive (less than half the length of the posterior seta) and by the antenna, with a plumose arista. The genus was revised by Davies & Miller (2008), which includes an identification key to the known Afrotropical species.

Prochaetops Bezzi (Lauxaniinae)**.** A genus with three described species, including two Oceanian species from Fiji and Guam. The single described Afrotropical species, *P. magnifica* (Bezzi, *in* Bezzi & Lamb, 1926), was described from Seychelles, although numerous undescribed species are known from throughout the region and elsewhere in the Old World. Several undescribed species are recognised from Madagascar. According to Stuckenberg (1971), this species would belong to *Panurgopsis*, having incorrectly considered *Prochaetops* as a junior synyonym. *Prochaetops* is characterised by being small-sized, having a frons that is horizontal in the same plane with the mesonotum, a receding face at a distinct angle with the frons, a black orbito-antennal macula, the anterior fronto-orbital seta being inclinate and very close to the lunule, the weak ocellar setae, the head usually being longer than high or subequal and often with a dark mark in the upper anterior corner of the katepisternum.

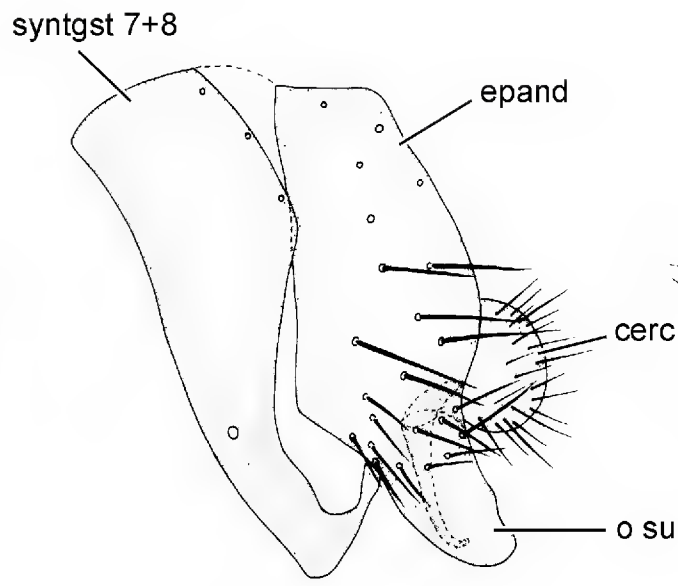
Prosamyza Stuckenberg (Lauxaniinae)**.** An endemic monotypic genus known from the single species, *P. viridiventris* Stuckenberg, 1971, described from South Africa. Like other genera related to *Minettia*, the genus has an intra-alar seta, but within this group, this is the only genus lacking a presutural dorsocentral seta (although a few species do have this seta) and with the anterior fronto-orbital seta being inclinate.

Proteaphila Davies & Miller (Lauxaniinae)**.** An endemic genus of three described species: *P. maculosa* Davies & Miller *in* Davies *et al*., 2012, *P. pajori* Davies, Miller & Muller, 2012 and *P. stuckenbergorum* Davies & Miller *in* Davies *et al*., 2012, all described from South Africa. Species of the genus are among the larger lauxaniids, being up to 6 mm in length, with a robust and compact body form. As in *Dyticomyia*, the genus has an auxiliary vein along wing vein M_1 extending into cell m_1 (although *Dyticomyia* has two such veins). The wing membrane is either darkened in the anterior part or has a reticulated pattern throughout. The genus is otherwise characterised by the frons projecting forward well beyond the eye margin, the face receding at an acute angle from the frons, the eye being elongate in the horizontal plane, presence of a dark fascia between the anterior eye margin and the upper parafacial and the presence of a presutural dorsocentral seta. As the genus name implies, there appears to be a strong connection between these flies and the botanical genus *Protea*, or Fynbos habitats. According to Davies *et al*. (2012), species of the genus appear to be restricted to high elevations (> 1000 m) temperate grasslands and forests along the Great Escarpment in eastern South Africa, but occurring at lower elevations (< 1000 m) in the Cape Floristic Region (Fynbos Biome) of the Western Cape. Despite the clear association with *Protea*, the biology and immature stages remain unknown. Davies *et al*. (2012) provided an identification key to the three described species.

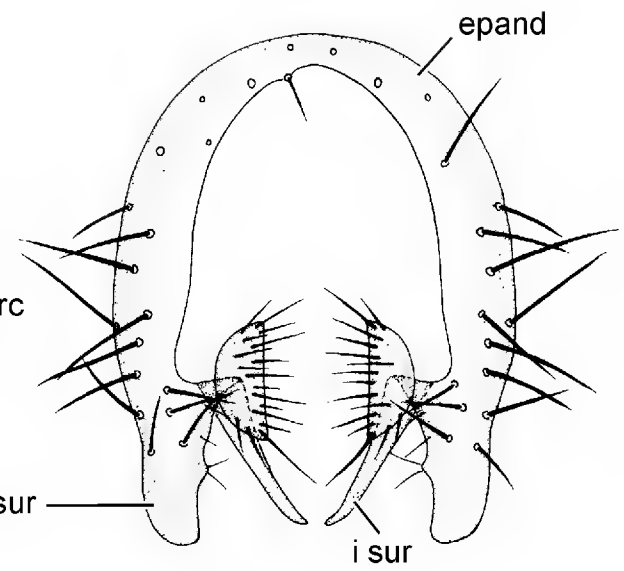
Sapromyza Fallén (Lauxaniinae)**.** The Afrotropical species currently recognised as representatives of this genus are likely not "true" *Sapromyza*, as this is the largest "dumping-ground" genus in the family globally, with more than 300 described species (more than 600 species were originally described as



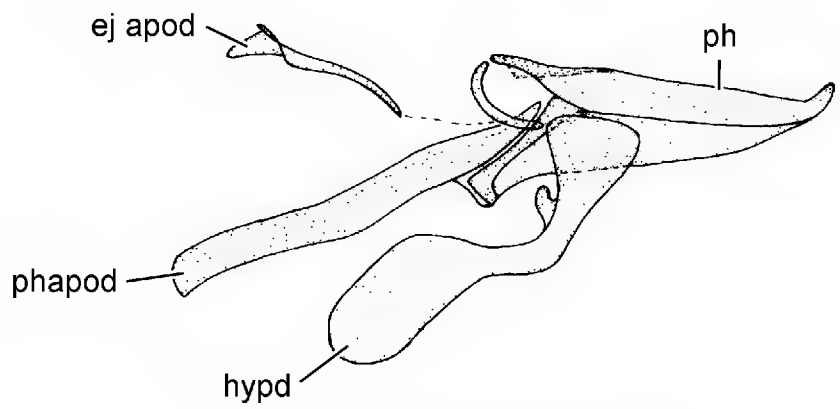
57 *Cestrotus* ♂



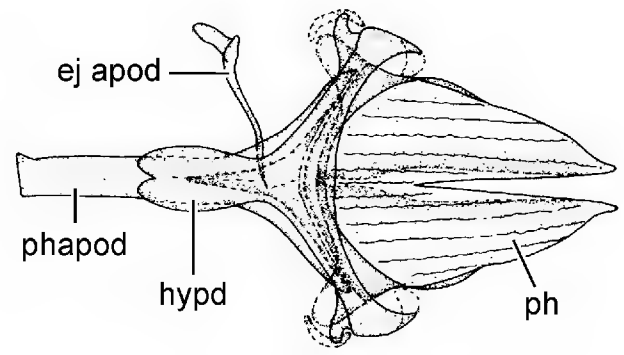
58 *Cestrotus* ♂



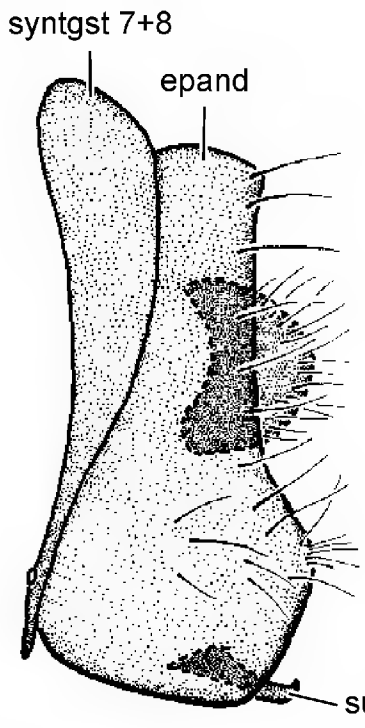
59 *Cestrotus* ♂



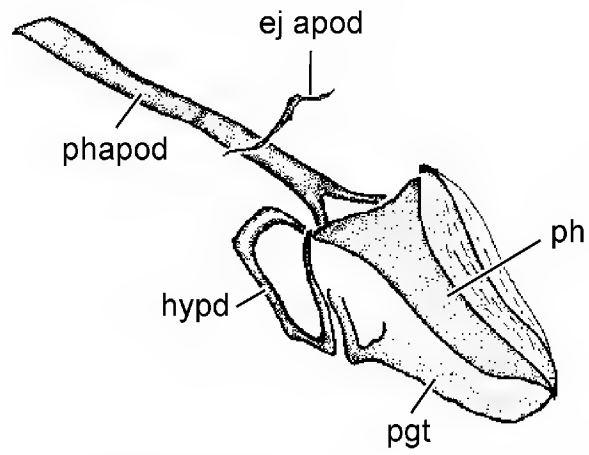
60 *Cestrotus* ♂



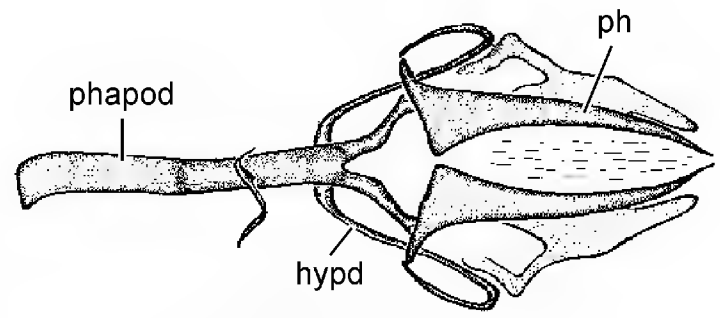
61 *Cestrotus* ♂



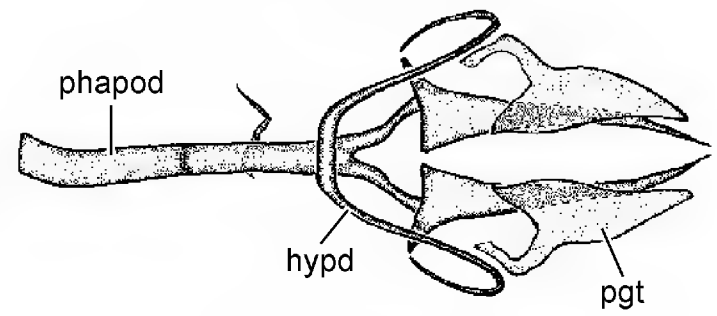
62 *Parapachycerina* ♂



63 *Parapachycerina* ♂



64 *Parapachycerina* ♂



65 *Parapachycerina* ♂

Figs 74.57–65. Male terminalia of Lauxaniidae: (57) syntergosternite 7 + 8 of *Cestrotus flavoscutellatus* de Meijere, anterior view (non-Afrotropical); (58) same, epandrial complex, lateral view; (59) same, dorsal view; (60) same, phallic complex, lateral view; (61) same, ventral view; (62) epandrial complex of *Parapachycerina munroi* Stuckenberg, lateral view; (63) same, phallic complex, dorsal oblique view; (64) same, dorsal view; (65) same, ventral view. Figs 57–61 (Shi *et al*. 2009, figs 33–37), Figs 62–65 (Davies & Miller 2008, figs 16, 20–22).

Abbreviations: cerc – cercus; ej apod – ejaculatory apodeme; epand – epandrium; hypd – hypandrium; i sur – inner surstylus; o sur – outer surstylus; pgt – postgonite; ph – phallus; phapod – phallapodeme; sur – surstylus; syntgst – syntergosternite.

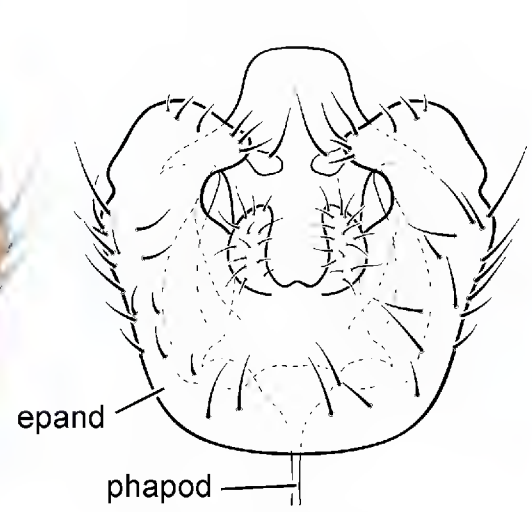
representatives of the genus). It is likely that the Afrotropical fauna has few, if any, true representatives, yet many specimens from all over the Afrotropics, including Madagascar and other Indian Ocean islands, are sorted to this name. This fact and the 12 currently valid species in this genus from the Afrotropics are a reflection of the need to reinterpret their true affinities. The Afrotropical species sorted to this genus have a flat, usually dull face, the fronto-orbital plates are neither broad nor glossy, with the fronto-orbital setae distributed more or less equally from the vertical setae to the lunule. As for mesonotal setae, the posthumeral seta is present and the intra-alar and presutural dorsocentral setae are absent. On the head, the frons and face are subequal, so the antenna is positioned at about the midpoint of the head, with the antennal arista being pubescent, the frons gently arched or flat and the ocellar triangle not demarcated by a macula. The genus is in need of revision to work out the true affinities of the species currently contained.

Spathecerus Lindner (Lauxaniinae)**.** An endemic monotypic genus known from the single species, *S. multipunctatus* Lindner, 1956, described from Tanzania. The genus is characterised by its flat, dull face, the dorsocentral setae arranged 1 + 3, the absence of an intra-alar seta, the strong ocellar setae, its heavily maculate body, an antennal postpedicel that is subtriangular (being broad basally and converging to the tip), an enlarged and protruding clypeus, the anterior fronto-orbital seta being inserted at the anterior margin of the frons and the frons being flattened to concave, with the face receding below at an angle.

Teratolauxania Stuckenberg (Lauxaniinae)**.** An endemic monotypic genus known from the single species, *T. cybeplax* Stuckenberg, 1971, described from South Africa. The genus is characterised in having a head that is distinctly higher than long, with the frons concave and descending steeply from the vertex and much higher than the face, such that the antennae are positioned low on the head, by having the wing flexed and held over the abdomen, having wing vein R_{2+3} curved towards and closely associated with the costal vein (C) and having small fronto-orbital setae, both on the posterior half of the frons.

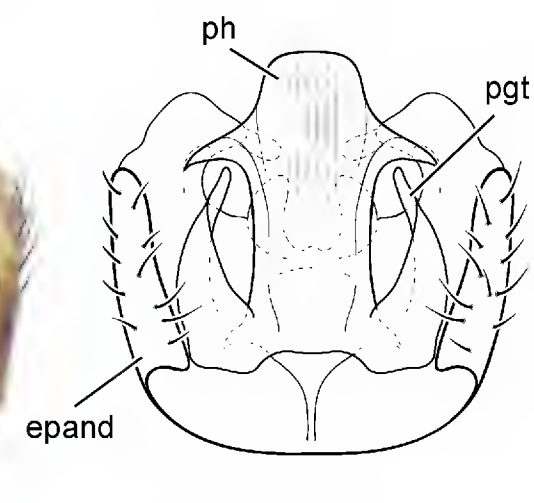
Trypetisoma Malloch (Homoneurinae)**.** A widespread genus of 56 described species occurring in all zoogeographical regions, except Antarctica. In the Afrotropics, the genus is currently known from a single described species, *T. perpunctata* (Lamb, 1912), from Seychelles, but there are numerous undescribed species known from across the region, including Madagascar and other Indian Ocean islands. As with other homoneurine genera, this genus has the costal spinules extending fully to wing vein R_{4+5}, although in some New World species these only extend slightly beyond vein R_{2+3}. The genus is characterised by the downsloping seta near the middle of

66 *Proteaphila* ♂



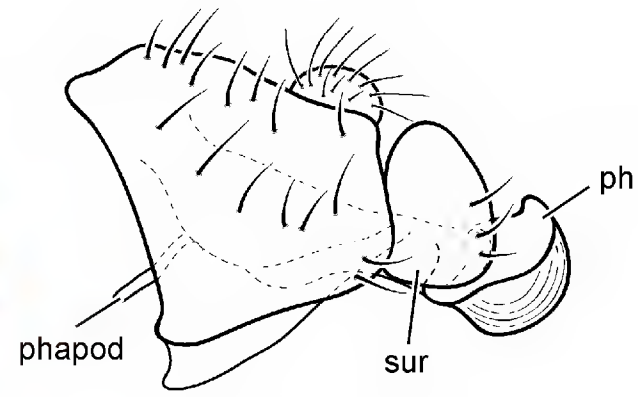
67 *Proteaphila* ♂

68 *Proteaphila* ♂



69 *Proteaphila* ♂

70 *Proteaphila* ♂



71 *Proteaphila* ♂

Figs 74.66–71. Male terminalia of Lauxaniidae: (66) *Proteaphila stuckenbergorum* Davies & Miller, dorsal view; (67) same; (68) same, ventral view; (69) same; (70) same, lateral view; (71) same. Figs 66–71 (Davies *et al*. 2012, figs 11A–C).

Abbreviations: epand – epandrium; pgt – postgonite; ph – phallus; phapod – phallapodeme; sur – surstylus.

the anepisternum (in addition to the anepisternal seta on the posterior margin), dorsocentral setae arranged 1 + 3, with a row of distinct acrostichal setae (in addition to a distinct presutural acrostichal seta) and a strongly patterned or irrorated wing. Although size has previously been used to differentiate the nominal subgenus (being quite small-bodied) from another (larger-bodied) subgenus, *T.* (*Trypaneoides* Tonnoir & Malloch), there are no reliable characteristics to separate them, so only the genus is recognised here.

Undescribed genus A (Lauxaniinae)**.** No Afrotropical species are currently assigned to the subgenus *Meiosimyza* (*Lyciella*), but many undescribed species from throughout the Afrotropics (including Madagascar), are superficially recognisable as such. It is unlikely, however, that the Afrotropical fauna has any true representatives of this Holarctic genus and these species are here considered to be an undescribed genus, so as not to cause future confusion with the identity of these undescribed species. This is a reflection of the need to determine their true affinities, which may result in one or more new genera, but it is currently not possible to further address the issue. The Afrotropical species sorted here (which includes *Sapromyza rhodesiella* Curran, 1938), have a flat dull face, dorsocentral setae arranged 1 + 3, lack an intra-alar seta, have strong ocellar setae, the body is not heavily marked, usually yellowish to grey, the anterior fronto-orbital setae are set back from the anterior margin of the frons and the frons is arched and evenly sloping into the plane of the face. Some species have the frons densely setulose anteriorly (as in the Asian genus *Hendelimyza* Frey), which may represent a different genus from those lacking setulae.

Undescribed genus B (Lauxaniinae)**.** This undescribed genus is known only from South Africa, where numerous specimens are known from different parts of the country. This material may represent more than one species. The genus has a flat, dull face and a presutural dorsocentral seta is present along with two postsutural dorsocentral setae. The undescribed species of this genus are further characterised by the head and eye being higher than long, both fronto-orbital setae being reclinate, the ocellar setae being strong, with a faint brown median stripe on the otherwise yellow frons and a yellow body with a pair of distinct dark brown vittae on the mesonotum through the scutellum.

Undescribed genus C (Lauxaniinae)**.** This undescribed genus is known only from Uganda from a few specimens. The genus is small-sized, with a flat, dull face and a presutural dorsocentral seta is present along with three postsutural dorsocentral setae. The single undescribed species of the genus is further characterised by a subtriangular antennal postpedicel with a subapical plumose arista, which has a cluster of elongated ventrobasal microtrichia. This species also has an enlarged and protruding clypeus, the anterior part of the frons is setulose and the anterior fronto-orbital seta is inclinate and located on the margin of the lunule.

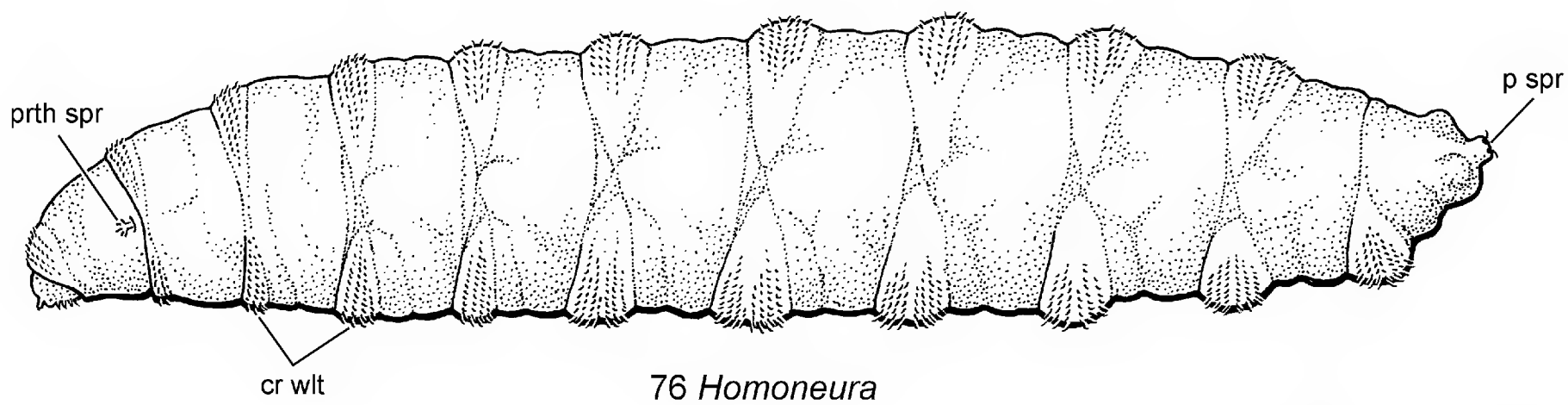
Undescribed genus D (Lauxaniinae)**.** This undescribed genus is known only from Madagascar from a single specimen.

Figs 74.72–75. Living immature stages of Lauxaniidae: (72) living third-larval instar (immobile) of undetermined Lauxaniidae (non-Afrotropical); (73) same (mobile); (74) living puparium of undetermined Lauxaniidae, dorsal view (non-Afrotropical); (75) same, ventral view. Figs 72–75 (photographs © W.P. Pfliegler).

The single undescribed species has a flat, dull face and a metallic blue body and lacks a presutural dorsocentral seta and is further characterised by the head being distinctly higher than long, having a broad gena and parafacial, the frons having a distinct transverse depression, both fronto-orbital setae being located in the posterior half of the frons, with the anterior seta smaller than the posterior and located at mid length of the frons and the antennae being widely separated.

Xangelina Walker (Lauxaniinae)**.** An Old World genus of seven described species occurring in the Afrotropical and Oriental Regions. Three species occur in the Afrotropics: *X. bequaerti* (Curran, 1938) in West Africa; *X. bimaculata* (Adams, 1905) in Southern Africa; and *X. submetallica* (Loew, 1862) is more widespread, occurring along the entire eastern section of the Afrotropics, from South Africa to Ethiopia. Undescribed species are known from throughout the region, including Madagascar. Representatives of this genus are characterised by their yellow to yellowish brown colour, having a glossy and evenly convex face, broad and glossy fronto-orbital plates and lacking ocellar setae. Curran (1938) provided an identification key to the three described Afrotropical species, albeit as representatives of the genus *Afrolauxania* Curran, now a junior synonym of *Xangelina*.

Zanjensiella Stuckenberg (Homoneurinae)**.** An uncommonly encountered endemic genus of two species: *Z. argentifrons* Stuckenberg, 1971 and *Z. canifrons* Stuckenberg, 1971, both confined to Madagascar. As with other homoneurine genera, the genus has the costal spinules extending fully to wing vein R_{4+5}. The genus is easily recognised by the unique face projecting ventrally as a silvery pruinose lobe over the clypeus and the plumose antennae. The biology and immature stages remain unknown. Although no identification key was provided, Stuckenberg (1971) thoroughly described both species.



Figs 74.76–81. Immature stages of Lauxaniidae: (76) habitus of third-larval instar of *Homoneura* sp., lateral view (non-Afrotropical); (77) same, prothoracic spiracle, lateral view. (78) same, cephaloskeleton, ventral view; (79) same, lateral view; (80) same, terminal segments, posterior view; (81) same, posterior spiracle, posterior view. Figs 76–81 (Shewell 1987, figs 66, 67, 70, 68, 69, respectively).

Abbreviations: cr wlt – creeping welts; d brg – dorsal bridge; d corn – dorsal cornu; den scl – dental sclerite; ep scl – epistomal sclerite; int scl – intermediate sclerite; lab scl – labial sclerite; mhk – mouthhook; p spr – posterior spiracle; pastm b – parastomal bar; prth spr – prothoracic spiracle; spic – spicules; spr op – spiracular opening; v corn – ventral cornu.

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CELYPHIDAE 75

(Beetle Flies)

Stephen D. Gaimari and Raymond M. Miller

Fig. 75.1. Female of *Spaniocelyphus* sp. (non-Afrotropical) (photograph © S.D. Gaimari).

Diagnosis

[Based on *Spaniocelyphus*, the only genus in the region].

Small- to moderately large-sized (3–8 mm) acalyptrate flies (Fig. 1); compact-bodied, with distinctly enlarged convex scutellum, extending over entire abdomen (Figs 1–5); usually metallic blue (Figs 2, 3) or green, reddish, bronzish (Fig. 1), yellowish (Fig. 4) or brownish (Fig. 5); integument smooth (although scutellum may be punctate or rugose in some species), with setulae sparse or absent and setation reduced.

Head smooth and shiny (Fig. 7), with vertex sharpened (Figs 6, 7) or rounded; frontal plates broad, from ocelli to lunule, turned up along lunule (Fig. 6); lunule narrow with distinct ptilinal fissure (Fig. 7); antenna (Fig. 6) with pedicel exposed, subequal to scape, postpedicel usually shorter than pedicel + scape, with antennal arista usually subapical, either setaceous or flattened and leaf-like in basal ½–¾ (Fig. 6); face flattened or convex (Fig. 6); clypeus enlarged, protruding forward (Fig. 6); setae absent or reduced, setula-like (if present, including minute inner and outer vertical setae, convergent postocellar setae, proclinate, erect or reclinate posterior fronto-orbital seta and inclinate to proclinate anterior fronto-orbital seta located immediately above antennal bases) (Fig. 7).

Thorax with mesonotum smooth (Fig. 1) or rugose (Fig. 3); setae absent or much reduced and inconspicuous, when present conforming to setal patterns found in Lauxaniidae (see Chapter 74); mesonotum short, with scutellum longer and broader, either only slightly broader (Fig. 3) or much broader (Fig. 5). Scutellum (Figs 2–5) much enlarged, distinctively

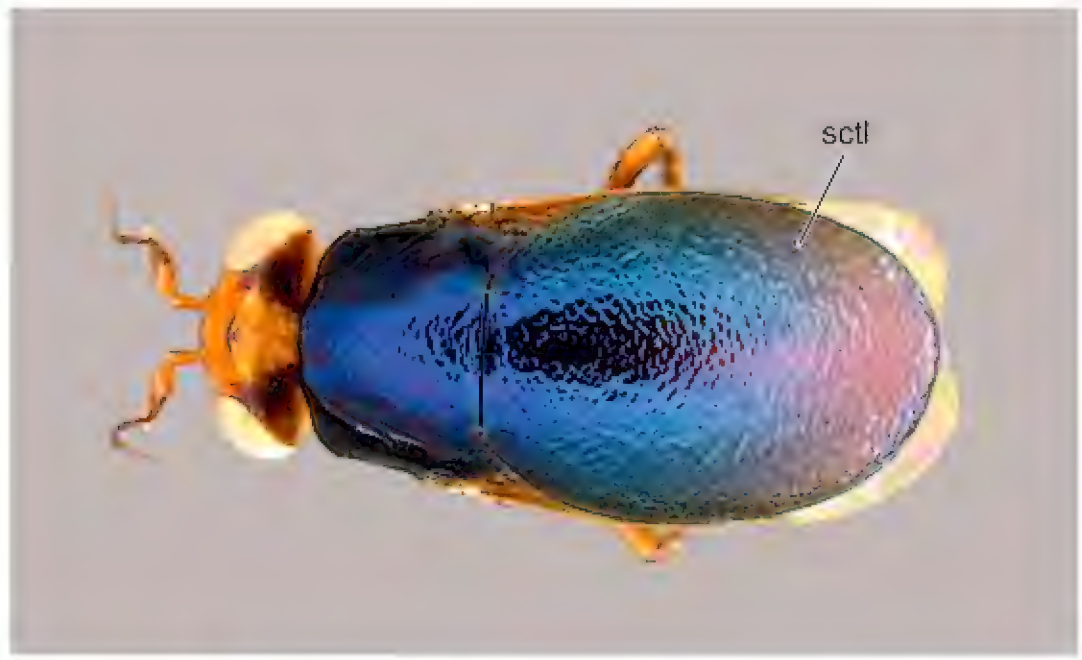
Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2021. Manual of Afrotropical Diptera. Volume 3. Brachycera—Cyclorrhapha, excluding Calyptratae. *Suricata* 8. South African National Biodiversity Institute, Pretoria; pp. 1783–1790.

convex, extending over abdomen, smooth, rugose or punctate. Wings at rest folded under scutellum (Figs 1, 5); membrane hyaline (Figs 10, 11); costal vein (*C*) unbroken, weaker beyond vein R_{4+5}, but ending at vein M_1 (Figs 10, 11); subcostal vein (*Sc*) appearing incomplete, with clearly discernible part straight, ending before curve of vein R_1, but continuing as a fold to costal vein (*C*) separated from vein R_1 (Fig. 12); veins R_{4+5} and M_1 convergent near middle of wing, with very short crossvein *r–m* (Figs 10, 11), crossvein *bm–m* present (Fig. 10) or absent; cell *cua* small with rounded apex (Figs 10, 11); vein *CuA+CuP* short (Fig. 10); alula large (Fig. 10), often folded under wing (Fig. 13). Legs with long, thin, setula-like anterior preapical seta on at least fore tibia (Fig. 8) and hind tibia (Fig. 9); hind tibia with small ventral spur (Fig. 9).

Abdomen smooth and shiny, broad and heavily sclerotised; tergites saddle-shaped, with lateral edges extending to ventral part of abdomen (Figs 18, 20, 21); abdominal segments 2 and 3 very large; tergites entire (Figs 15, 16) or subdivided into three broad sections, with dorsolateral longitudinal sutures dividing each tergite (Fig. 14); male abdominal sclerites 7 and 8 often fused into closed ring (syntergosternite 7 + 8), surrounding the terminalia (Fig. 18), or ring open ventrally; epandrium horse-shoe shaped (Fig. 19), with articulated surstyli (Figs 18, 19); phallus membranous and indistinct, or indiscernible; paired median postgonites (referred to as gonapophyses or pregonites in some published works) large and distinct (Figs 18, 19); pregonite absent; females syntergosternite 7 fused into closed ring, either broadly open (Fig. 20) or forming narrow slit (Fig. 21); sternite 8 enlarged (Figs 20, 21), with distinct epiproct, hypoproct and short cerci (Fig. 20); internally, spermathecae globular, in conformation 1 + 2 (Fig. 22).

Egg (Figs 23, 24) 1 mm in length or less, 0.2–0.4 mm in width; white, ovoid, blunt at both ends; anteriorly rounded or with distinct tubercle shielding apical micropyle; posteriorly with knob-like swelling or constricted tubercle; chorion with series of distinct longitudinal ridges, with fine transverse striations or septa between.

2 *Spaniocelyphus*



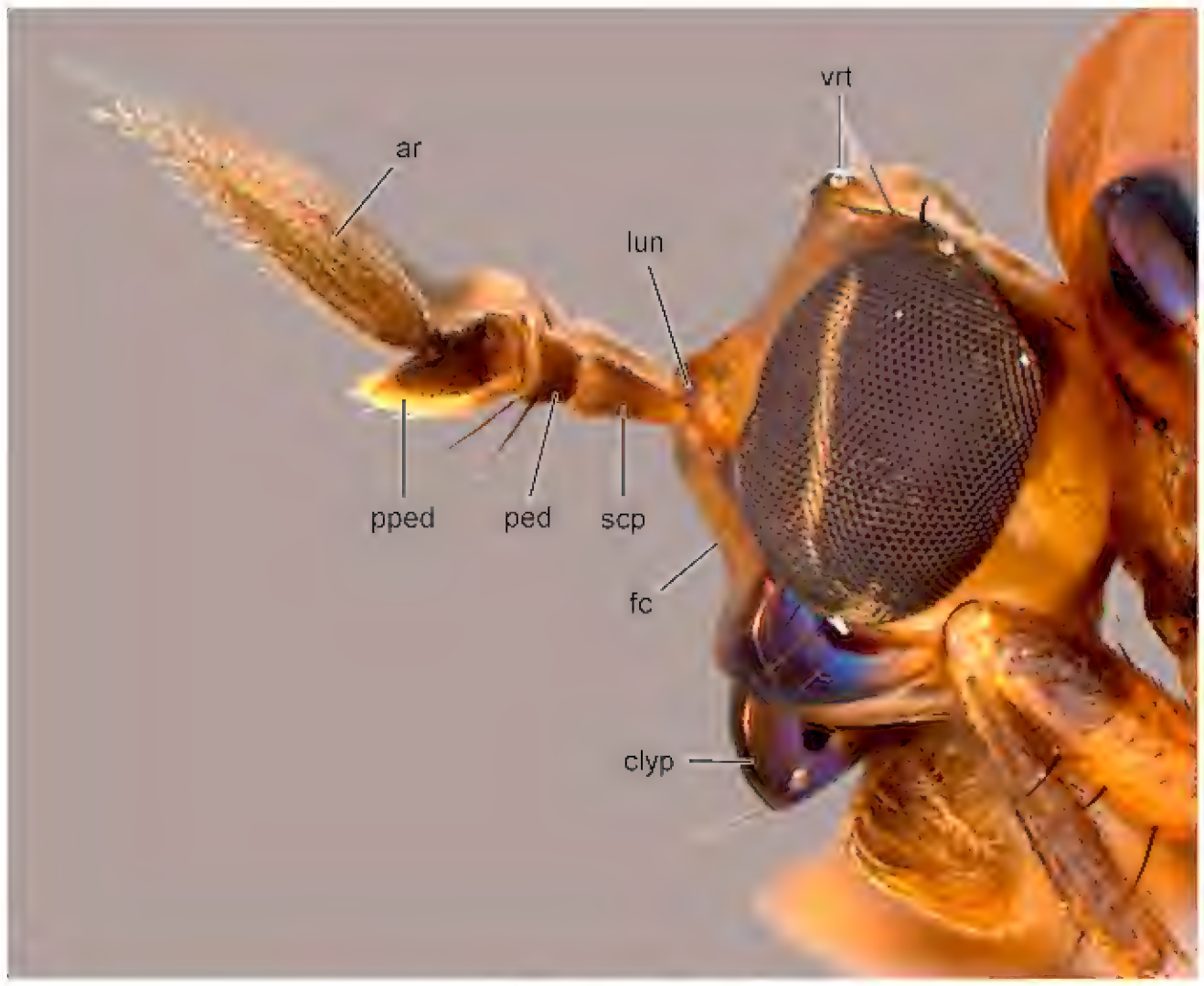
3 *Spaniocelyphus*

4 *Spaniocelyphus*

5 *Celyphus*

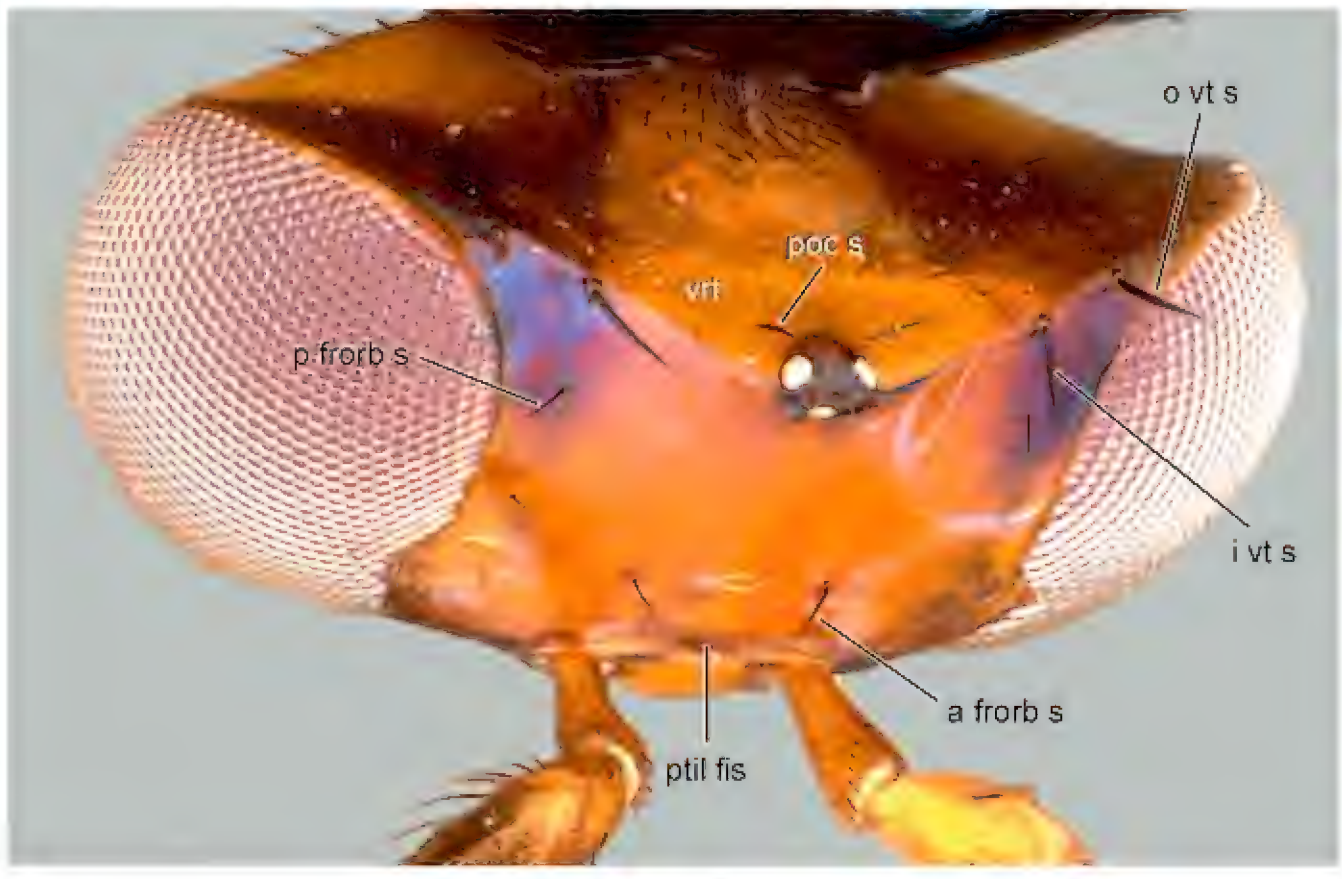
Figs 75.2–5. Habitus of Celyphidae: (2) *Spaniocelyphus* sp., lateral view ♀; (3) same, dorsal view; (4) same, lateral view; (5) habitus of living *Celyphus* sp. ♀ (non-Afrotropical). Fig. 5 (photograph © S.D. Gaimari).

Abbreviation: sctl – scutellum.

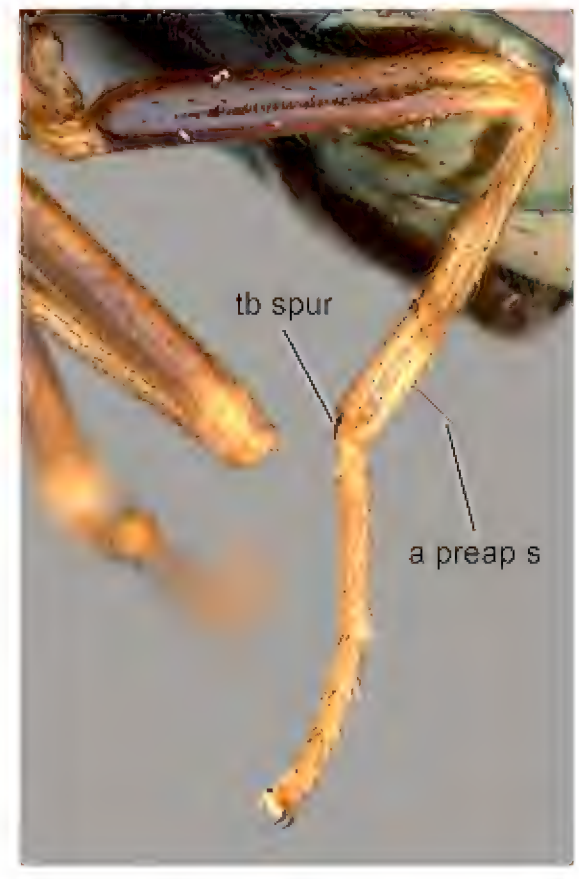


6 *Spaniocelyphus*

8 *Spaniocelyphus*



7 *Spaniocelyphus*



9 *Spaniocelyphus*

Figs 75.6–9. Heads and legs of Celyphidae: (6) head of *Spaniocelyphus* sp., lateral view ♀; (7) same, frons, dorsal view; (8) same, fore leg, lateral view; (9) same, hind leg, lateral view.

Abbreviations: a frorb s – anterior fronto-orbital seta; a preap s – anterior preapical seta; ar – arista; clyp – clypeus; fc – face; i vt s – inner vertical seta; lun – lunule; o vt s – outer vertical seta; p frorb s – posterior fronto-orbital seta; ped – pedicel; poc s – postocellar seta; pped – postpedicel; ptil fis – ptilinal fissure; scp – scape; tb spur – tibial spur; vrt – vertex.

Larva (Figs 25, 28) white, translucent with white fat globules evident; elongate, cylindrical, tapering at both ends with abdominal segments 3–6 subequal and broadest.

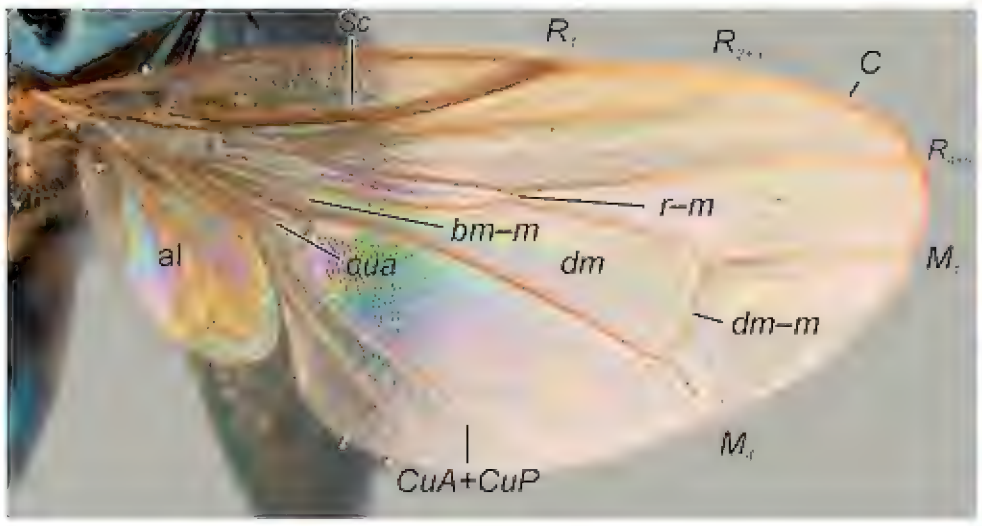
Puparium (Figs 26, 27, 29, 30) spindle-shaped (in dorsal view), widest medially (puparium of *Spaniocelyphus scutatus* (Wiedemann, 1830) (Fig. 29) distinctly narrower than that of *Celyphus obtectus* Dalman, 1818 (Fig. 26), relative to respective widths of scutella); markedly flattened ventrally (as surface adheres to substrate); highly convex medially, sharply tapered at both ends.

Celyphidae are easily recognised by their enlarged convex scutellum, being longer than the mesonotum and extending over the entire abdomen (the exception being the mainly Philippine genus *Idiocelyphus* Malloch, in which the scutellum and mesonotum are subequal). This, along with their metallic colouration and ability to tuck the wings under the enlarged scutellum, makes their habitus much like certain small metallic chrysomelid beetles. Very few families have genera that even superficially resemble celyphids, although one Afrotropical genus of Chloropidae (see Chapter 96), was originally described as a celyphid (*Afrocelyphus* Vanschuytbroeck, now considered a junior synonym of *Nomba* Walker).

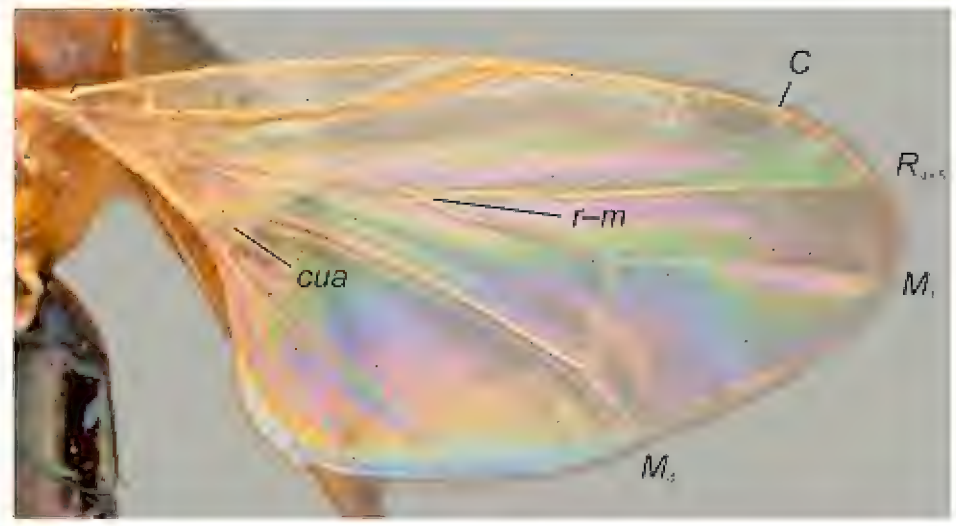
Biology and immature stages

Adult celyphids occur in moist habitats where they are found walking on vegetation. They are most commonly encountered in wet grassy habitats, where they can be quite abundant, but certain celyphids (e.g., *Paracelyphus* Bigot species) can be found walking on leaves and thick stems of broad-leafed plants such as banana. These wet habitats are particularly rich in decaying plant material, where the larvae feed.

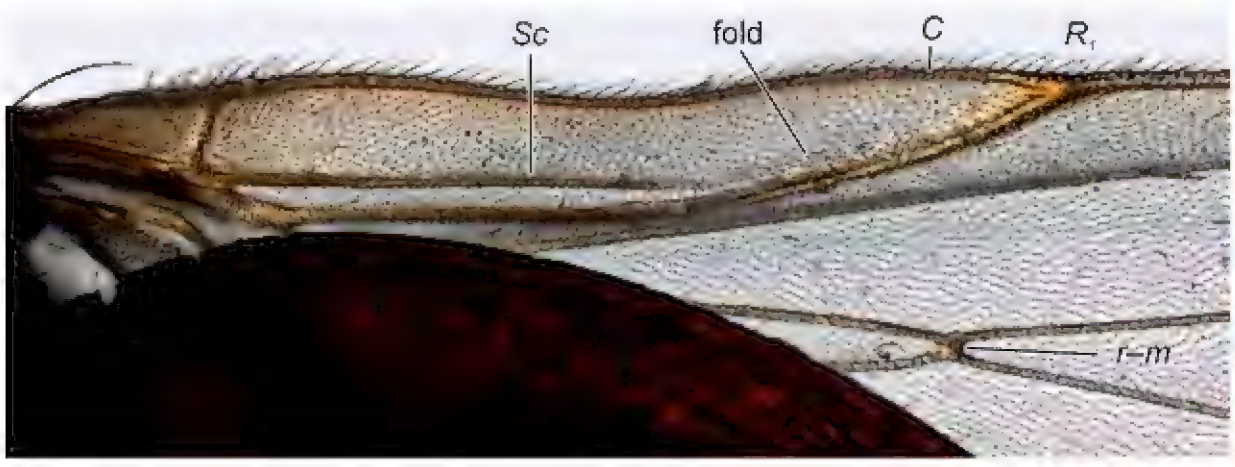
Very little information has been published on the biology and immature stages of Celyphidae. The only significant work was that of Sen (1921), which discussed and illustrated the immature stages of the Asian species *Spaniocelyphus scutatus* and *Celyphus obtectus*. This paper was the origin of our understanding that celyphids, as with Lauxaniidae, feed in decaying plant matter, which is also corroborated by label data from reared specimens. Sen (1921) reported that eggs of *C. obtectus* are laid along veins on the underside of older green or yellowing leaves. A single female can lay as many as 60–70 eggs, which are deposited singly. Larvae occur on the upper surface of these leaves and feed within the decaying parts thus skeletonising them. The habits of *S. scutatus* were much more difficult to observe, as these only rarely oviposit in captivity. The few that did lay eggs



10 *Spaniocelyphus*



11 *Spaniocelyphus*



12 *Spaniocelyphus*

13 *Spaniocelyphus*

Figs 75.10–13. Wings of Celyphidae: (10) *Spaniocelyphus* sp., dorsal view ♂; (11) *Spaniocelyphus* sp., dorsal view ♀; (12) same, anterior part of wing base; (13) same, wing base, ventral view ♀.

Abbreviations: al – alula; *bm–m* – basal median crossvein; *C* – costal vein; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *dm* – discal medial cell; *dm–m* – discal medial crossvein; M_1 – first branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Sc* – subcostal vein.

did so along the margins of grass blades, and in one case on a rotten leaf of a non-grass species. For Afrotropical species, Miller (1987) reported laboratory observations on the biology of *S. unsinduzi* Stuckenberg, 1960, from South Africa, having reared adults from collections in KwaZulu-Natal from moist areas in grasslands in the late summer. Larvae were fed on decaying grass and lettuce and the life cycle, egg through to adult eclosion, was 18 + days (egg stage, 2–4 days; first-instar larva, 2 + days; second-instar larva, 2 + days; third-instar larva, 3 + days; prepupal stage, *ca* 24 hours; puparial stage 6–8 days).

Economic significance

No species of economic significance are currently known.

Classification

Celyphidae are representatives of the superfamily Lauxanioidea, with a clearly close relationship to Lauxaniidae and may, in fact, be a subordinate group within that family. McAlpine (1989: 1444) considered celyphids as the sister-group of non-Afrotropical Eurychoromyiidae (both together being the sister-group of Lauxaniidae), but Gaimari & Silva (2010) revised the status of the latter to a subfamily of Lauxaniidae, not necessarily close to celyphids. Molecular phylogenetic works that have included celyphids and lauxaniids (e.g., Li *et al.* 2017) have suffered from a lack of broad taxon sampling (in the cited paper, only five lauxanioid taxa were sampled), so no topology beyond the sister-group relationship between the two families has been uncovered. Many earlier authors considered celyphids to be a subfamily of Lauxaniidae, but Tenorio (1972), in her excellent treatment of the entire Oriental fauna of the family, considered celyphids to be "… unique and discreet enough to deserve family distinction." This viewpoint is followed here, but with the caveat that they are likely a monophyletic lineage within the Lauxaniidae. Although considered a synapomorphy for Lauxaniidae (McAlpine 1989: 1444), celyphids also display the male accessory glands as a dense tangle, due to repeated branching (Sturtevant 1925, 1926) (Fig. 17), making this characteristic a synapomorphy for Lauxaniidae + Celyphidae. Several characteristics of the Celyphidae make them stand out from Lauxaniidae in general, although various lauxaniid genera share these characteristics, at least in part. For example, the extremely enlarged scutellum is unique to celyphids within Lauxanioidea, but a moderately enlarged scutellum is present in several lauxaniid genera, including the Oriental genera *Celyphohomoneura* Papp & Kim and *Lyperomyia* Frey and the Neotropical genus *Celypholauxania* Hendel and the scutellum of the Philippine celyphid genus *Idiocelyphus* is more in line with these lauxaniids. The flattened leaf-like arista (Fig. 6) is common to most celyphids, but can also be found to a lesser degree in such lauxaniid genera as *Cerataulina* Hendel and *Kertesziella* Hendel, in addition to the fact that some celyphid genera, such as *Hemigloblus* Frey and *Paracelyphus* have a setaceous arista and one genus, *Atopocelyphus* Gaimari has a short plumose arista. Even the apparent lack of a phallus (*i.e.*, the phallus is membranous) in the celyphids is found in some species of *Minettia* Robineau-Desvoidy, in the Lauxaniidae.

14 *Spaniocelyphus*

15 *Celyphus*

16 *Celyphus*

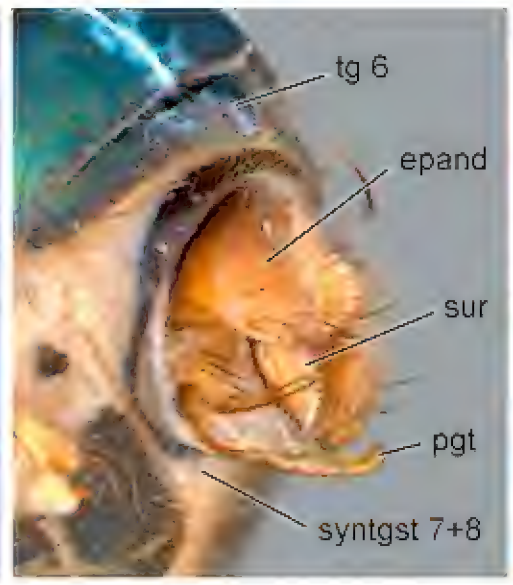
Figs 75.14–16. Abdomens of Celyphidae: (14) *Spaniocelyphus* sp., posterodorsal view ♀; (15) basal abdominal segments of *Celyphus rugosus* Tenorio, dorsal view ♂ (non-Afrotropical); (16) same, distal abdominal segments, posterodorsal view.

Abbreviation: long sut – longitudinal suture.

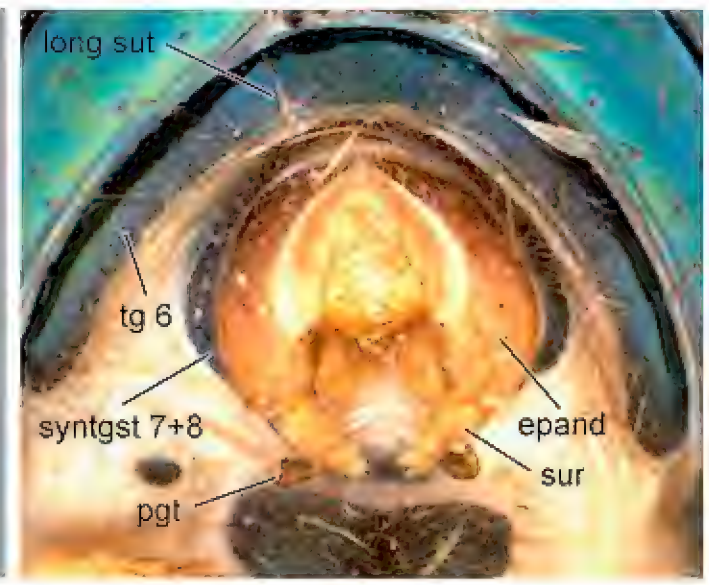
Identification

Currently the family comprises 115 valid species in eight genera, with most of that diversity found in tropical Asia and Southeast Asia. The exceptions are one monotypic genus in the Neotropical Region (Gaimari 2017) and 12 species in one genus in the Afrotropical Region. The several works of Frey (1941) and Vanschuytbroeck (1952, 1953*a*, *b*, 1959, 1963) were the only synthetic taxonomic works that dealt with Afrotropical celyphids, addressing both new species and the previously described species. For both authors, all of the Afrotropical species were considered to be representatives of the strictly Afrotropical genus *Chamaecelyphus* Frey and each of these works included an identification key to the species known up to that point. Stuckenberg (1960) also described two Afrotropical species, but parted with Vanschuytbroeck in considering them to be representatives of the otherwise tropical Asian genus *Spaniocelyphus* Hendel. These species are all treated in the Afrotropical catalogue of Miller (1980). Starting with Frey (1941), *Chamaecelyphus* was differentiated from *Spaniocelyphus* based solely on the absence of crossvein *bm–m* on the wing (present in *Spaniocelyphus*), in addition to *Chamaecelyphus* being apparently restricted to the Afrotropics and *Spaniocelyphus* to tropical Asia. Stuckenberg (1960) had described two species that had a faint crossvein *bm–m* and regarded these as *Spaniocelyphus* for the first time in the Afrotropics. He further pointed out that the grounds for separating these two genera seemed very tenuous, which was also suggested by Miller (1987). After observing that this is not a consistent character, even within species, Gaimari (2017) synonymised *Chamaecelyphus* under *Spaniocelyphus*, leaving all Afrotropical celyphid species in *Spaniocelyphus*. An identification key to world genera of the

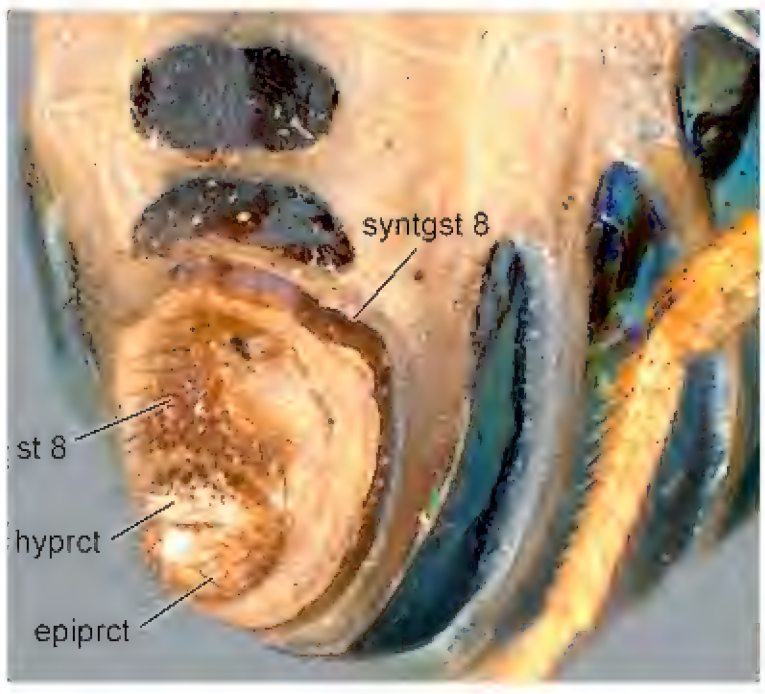
17 *Celyphus* ♂



18 *Spaniocelyphus* ♂

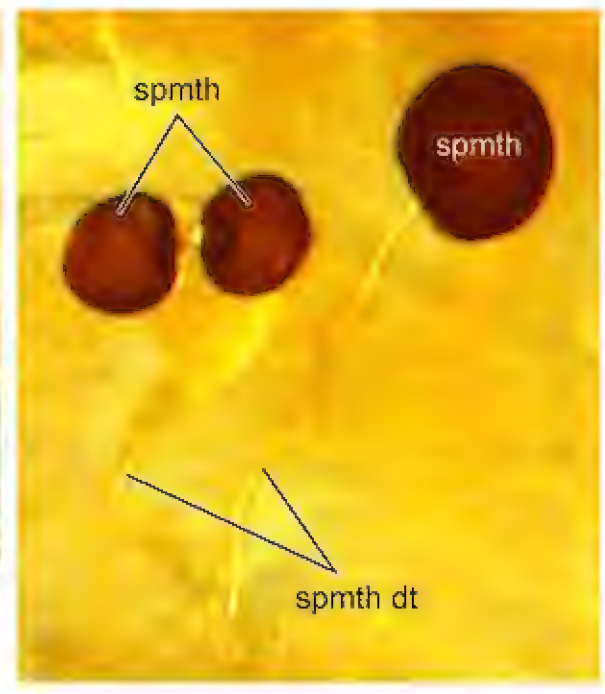


19 *Spaniocelyphus* ♂



20 *Spaniocelyphus* ♀

21 *Spaniocelyphus* ♀



22 *Celyphus* ♀

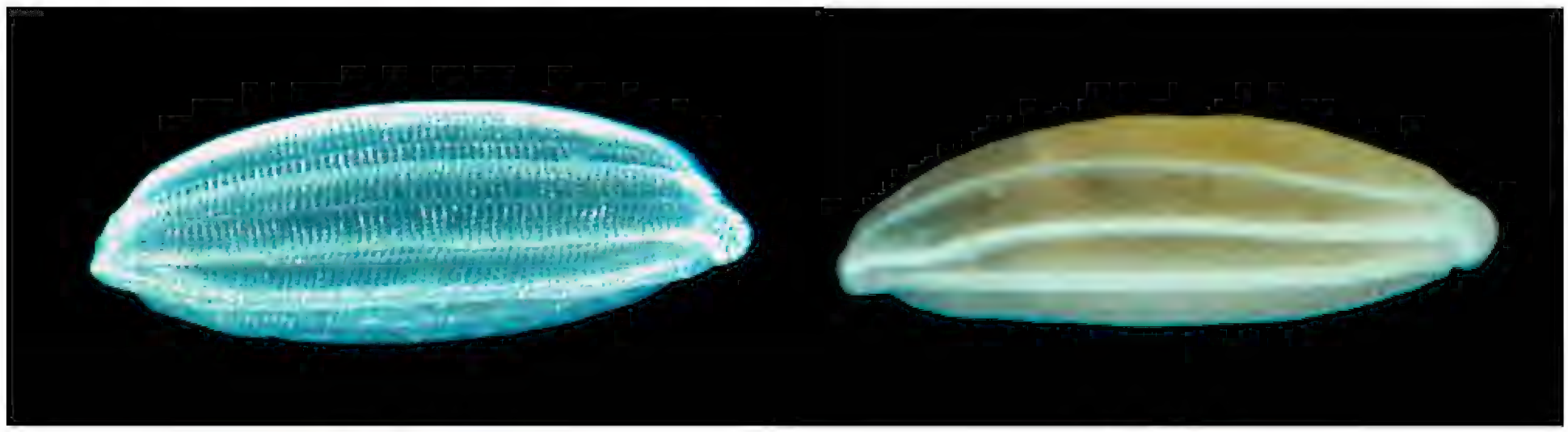
Figs 75.17–22. Male and female reproductive structures of Celyphidae: (17) male accessory glands of *Celyphus aurora* Karsch, dorsal view (non-Afrotropical); (18) male terminalia of *Spaniocelyphus* sp., ventral oblique view; (19) same, ventral view; (20) same, female terminalia, ventral oblique view; (21) same, ventral view; (22) spermathecae of *C. aurora*, lateral view (non-Afrotropical).

Abbreviations: acc gl – accessory gland; epand – epandrium; epiprct – epiproct; hyprct – hypoproct; long sut – longitudinal suture; pgt – postgonite; spmth – spermatheca(e); spmth dt – spermathecal duct; st – sternite; sur – surstylus; syntgst – syntergosternite; tg – tergite.

family was provided by Gaimari (2017), with relevant figures and discussion, and identification keys and figures for tropical Asian and South-east Asian species are given by Tenorio (1969, 1972). Vanschuytbroeck (1963) is the most recent work to include a key to species of the Afrotropics (albeit in the wrong genus), although the species described by Stuckenberg (1960) were missing. It should be noted when considering the species of Stuckenberg (1960) relative to those of Vanschuytbroeck and earlier authors that the crossvein *bm–m* character is not a useful one. Also important is the observation by Miller (1987) that teneral adults can take about five days before colouration and sculpturing is fully developed; before that time, identifications based on external morphology can be problematic. Celyphidae are best micro-pinned in the field for later double-mounting (see Chapter 2).

Synopsis of the fauna

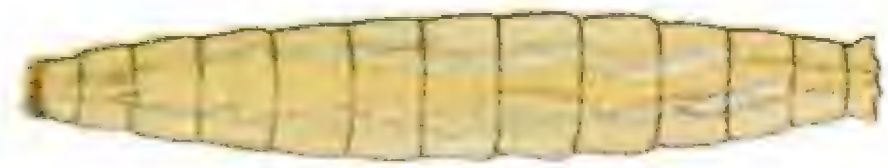
Afrotropical representatives of the family Celyphidae belong to the single genus *Spaniocelyphus* (Fig. 1).



23 *Celyphus*

24 *Celyphus*

25 *Celyphus*



28 *Spaniocelyphus*

26 *Celyphus*

29 *Spaniocelyphus*

27 *Celyphus*

30 *Spaniocelyphus*

Figs 75.23–30. Immature stages of Celyphidae (all non-Afrotropical): (23) egg of *Celyphus aurora* Karsch (slide-mounted), dorsal view; (24) egg (*in situ*) of *Celyphus* sp., dorsal view (non-Afrotropical); (25) third-instar larva of *C. obtectus* Dalman, left lateral view; (26) same, puparium, dorsal view; (27) same, puparium, left lateral view; (28) third-instar larva of *Spaniocelyphus scutatus* (Wiedemann), dorsal view; (29) same, puparium, dorsal view; (30) same, puparium, left lateral view. Fig. 24 (photograph © A. Kei C. Wong), Figs 25–30 (after Sen 1921, figs 2–4).

***Spaniocelyphus* Hendel.** A genus of 45 described species occurring in the Afrotropical (12 species) and Oriental (33) Regions. The genus is characterised by the carinate vertex of the head, the postocellar setae being tiny and setula-like, the antennal arista being flattened in the basal half to three-quarters and leaf-like and the division of abdominal tergites into three sections, with dorsolateral longitudinal sutures dividing each tergite. One species is widespread in the northern and central Afrotropics, *S. africanus* (Walker, 1849), is known from Senegal to Ethiopia in the north and to Democratic Republic of Congo to the south. Two species are known only from Southern Africa: *S. pamelae* Stuckenberg, 1960 from Mozambique and *S. umsinduzi* Stuckenberg, 1960 from South Africa to Zambia. The remaining nine species are all recorded from Central Africa, particularly Democratic Republic of Congo. No Afrotropical island species are known. The immature stages of Afrotropical species have not been described, but some biological information was reported by Miller (1987) for *S. umsinduzi*. An identification key to species was provided by Vanschuytbroeck (1963), including all ten species then known (as *Chamaecelyphus*), but did not account for the two species described subsequently in *Spaniocelyphus* by Stuckenberg (1960) and no taxonomic work has been published on Afrotropical Celyphidae since that time.

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CHAMAEMYIIDAE 76

(Silver Flies)

Stephen D. Gaimari

Fig. 76.1. Female of a *Leucopis* (*Leucopis*) sp. (non-Afrotropical) (photograph © C. Pilon).

Diagnosis

Small-sized (body length: 1.0–5.0 mm), compact-bodied (Figs 1, 8, 10, 12, 18), or elongate (Figs 2, 4, 6, 14, 16, 20, 22, 26) acalyptrate flies; usually densely silvery grey pruinose (Figs 8, 20), occasionally dark grey or brown (Fig. 24), or polished black (Fig. 16); often with brown to goldish vittae on mesonotum (Figs 5, 9, 11, 13) and/or brown to black pruinose maculae or fasciae on abdominal tergites (Figs 57–61).

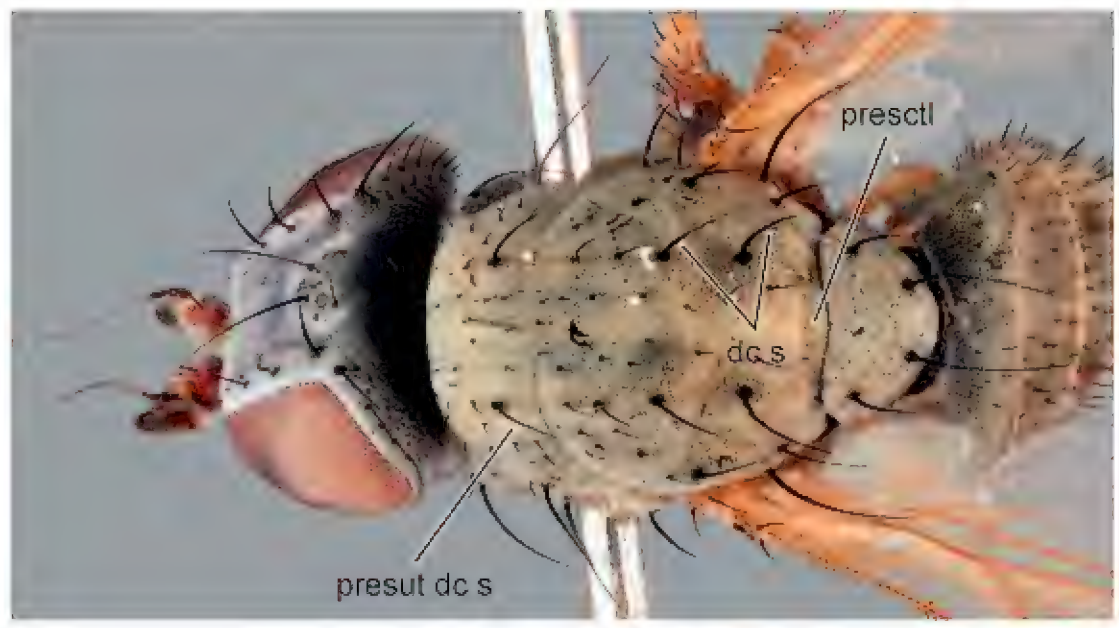
Head either compact, shorter than high, rounded anteriorly (Figs 33, 46–48), to subequal or longer than high, rounded or pointed anteriorly (Figs 44, 45, 49); postocellar setae convergent (Figs 28, 29) to subparallel (Figs 30, 32), or absent (Figs 34, 36); ocellar setae long, proclinate (Figs 29, 31, 33, 43), reduced and reclinate (Figs 39, 41), or absent (Figs 35, 37); fronto-orbital setae absent (Figs 35, 37, 39) or with 1 (Fig. 41) or 2 (Figs 29, 31, 32, 43) reclinate setae, in the last case either distributed evenly on frontal orbits (Fig. 31), or inserted posteriorly (Figs 41, 43, 48, 49); lunule small, narrowly exposed, bare (Figs 28, 30, 32, 42), to large and exposed (Figs 34, 38), to very large, broadly exposed and setulose (Figs 40, 41) or bare (Figs 36, 37); vibrissa absent (although pseudovibrissal seta may be enlarged, e.g., Figs 35, 39, 41); antenna short (rarely 2 × as long as high), porrect; postpedicel short and rounded (Figs 35, 37, 39, 41, 46–48), elongated and rounded (Fig. 49), or pointed and upturned apically (Figs 29, 31, 33, 45); arista subbasal, bare or short-pubescent, never plumose.

Thorax with mesonotum setulose; with 1–4 (rarely 5) dorsocentral setae, either all postsutural (Figs 7, 9, 11, 13, 19, 25, 27), or with 1 presutural (Figs 3, 5, 15, 17, 21, 23); 1 postpronotal, 1 presutural and 1 postsutural supra-alar, 2 postalar and 2 notopleural setae present; prescutellar acrostichal seta

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2021. Manual of Afrotropical Diptera. Volume 3. Brachycera—Cyclorrhapha, excluding Calyptratae. *Suricata* 8. South African National Biodiversity Institute, Pretoria; pp. 1791–1814.

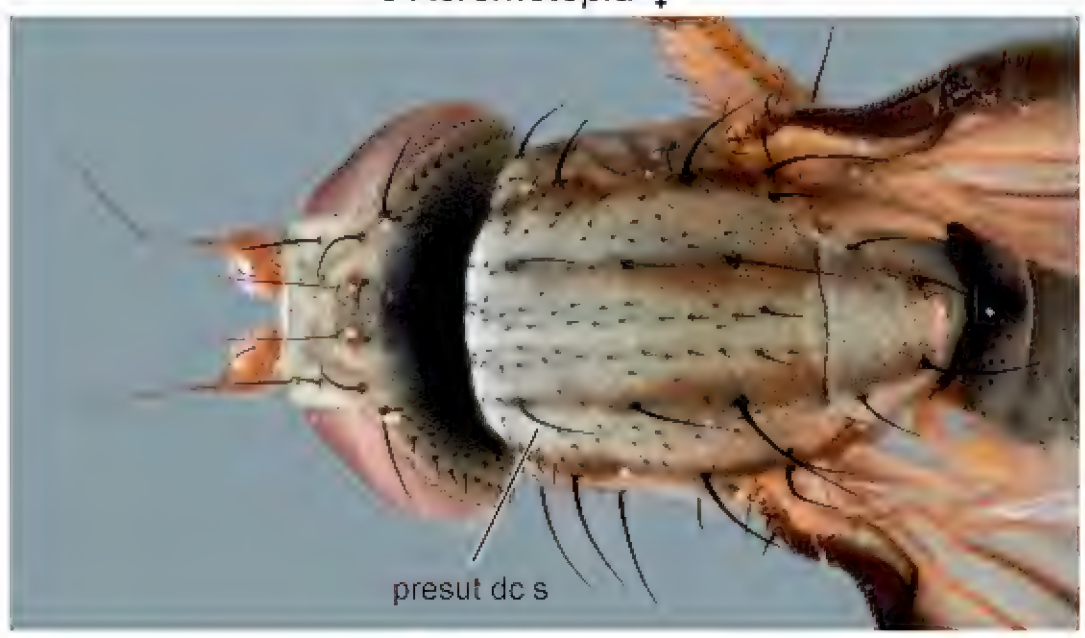
present or absent; prescutellum present (absent only in *Lipoleucopis* de Meijere); scutellum with 2 pairs of setae, otherwise bare; anepisternum with (Figs 8, 9, 15, 17, 22, 23), or without (Figs 4, 6, 10, 12, 20, 21, 24, 26) seta(e) or setulae; anepimeron bare; katepisternum with 1 strong seta in addition to setulae; proepisternal and proepimeral setae absent; prosternum bare. Wing (Figs 50–56) with costal vein (*C*) unbroken, extending to vein M_1 (to vein R_{4+5} in *Lipoleucopis*, Fig. 56); subcostal vein (*Sc*) complete, separated from vein R_1; basal medial cell (*bm*) and discal medial cell (*dm*) separated by crossvein *bm–m*;

2 *Acrometopia* ♀

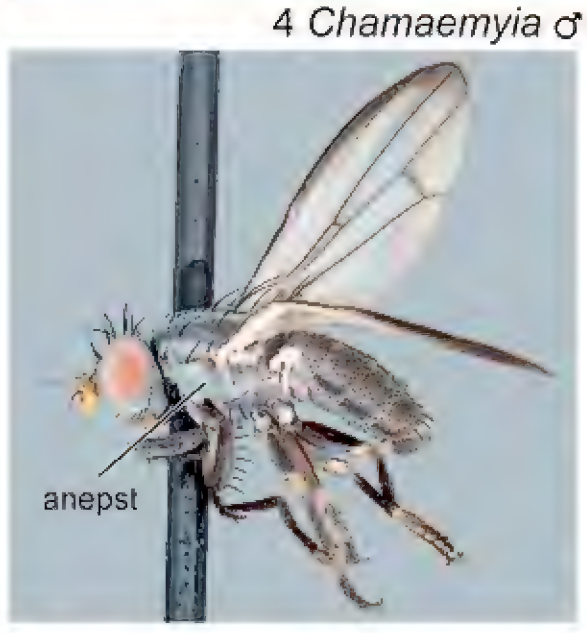


3 *Acrometopia* ♀

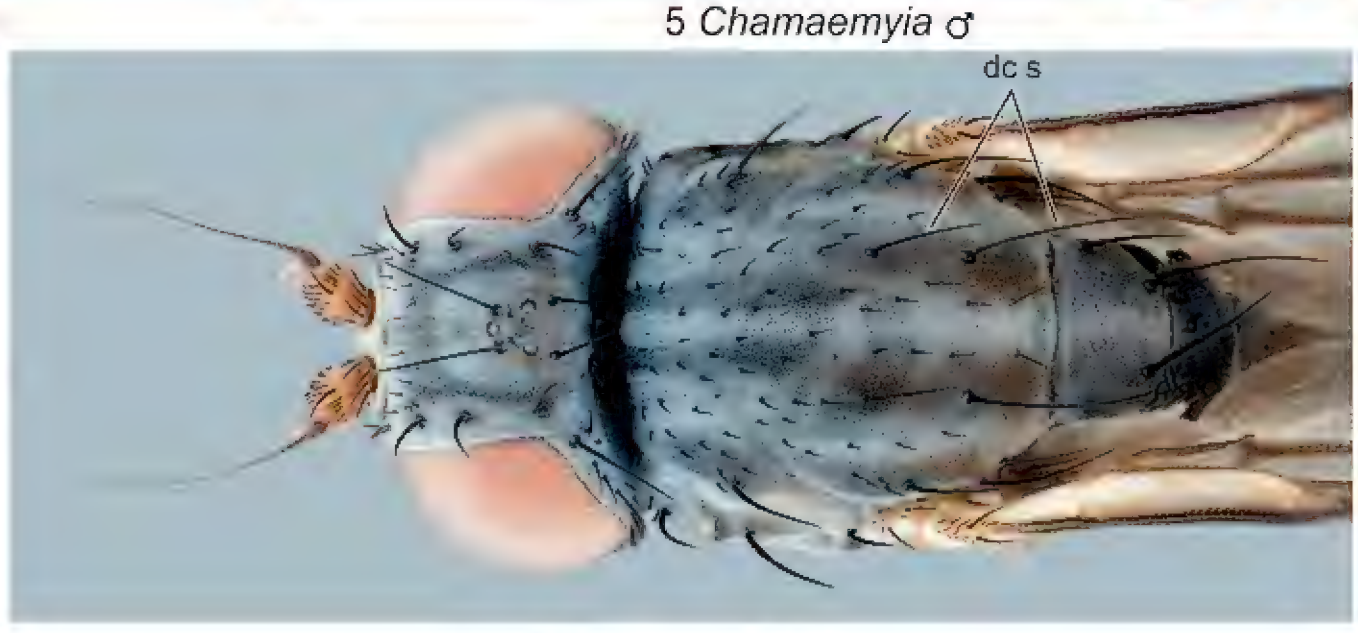
4 *Chamaemyia* ♂



5 *Chamaemyia* ♂



6 *Hamecamyia* ♂



7 *Hamecamyia* ♂

Figs 76.2–7. Habitus and heads and thoraces of Chamaemyiidae: (2) habitus of *Acrometopia* sp., lateral view ♀; (3) same, head and thorax, dorsal view; (4) habitus of *Chamaemyia* sp., lateral view ♂; (5) same, head and thorax, dorsal view; (6) habitus of *Hamecamyia stuckenbergi* Gaimari, lateral view ♂; (7) same, head and thorax, dorsal view. Figs 6, 7 (Gaimari 2012, figs 1, 2).

Abbreviations: anepst – anepisternum; dc s – dorsocentral setae; presut dc s – presutural dorsocentral seta; presctl – prescutellum.

anterior cubital cell (*cua*) present; vein *CuA+CuP* short, not reaching wing margin; membrane sometimes patterned (particularly along costal vein (*C*), e.g., some *Chamaemyia* Meigen, Fig. 51), hyaline or milky white. Legs without preapical dorsal tibial seta.

Abdomen short and compact (Figs 60–62) or elongate and tapering (Figs 57–59); tergites with large (Figs 57–59, 61), small (Fig. 60), or without (Fig. 62) paired brown to black pruinose maculae or fasciae; sternites simple, setulose (Fig. 63); male pregenital sclerites variable, including sternite 6 placed asymmetrically (Fig. 64), or reduced and placed symmetrically or asymmetrically, or absent; sternite 7 sometimes part of syntergite 7+8, or separate, reduced and placed symmetrically or asymmetrically, or absent; syntergosternite 7+8 sometimes incompletely fused and asymmetrical (Figs 64, 65), or completely fused and symmetrical, or symmetrical and greatly reduced (Leucopini); male terminalia with epandrium more or less rounded (Figs 64, 65); surstylus absent or fused to and extended out from epandrium (Fig. 64); hypandrium subcircular from dorsal aspect (Fig. 66), band-like from lateral aspect (Fig. 67); pregonite present (Fig. 67), or absent; postgonites present, elongated (Fig. 67); phallapodeme quadrate to subtriangular (Fig. 67); phallus tubular, not subdivided, with shape simple (Fig. 68) to complex; female terminalia usually with spermathecae in conformation 2 + 2, with 1 accessory gland (Fig. 69) (Neotropical *Echinoleucopis* Gaimari & Tanasijtshuk, display variation, due to fusion of one or both pairs of spermathecae).

Egg (Figs 70, 71) ovoid or elongate, either uniformly rounded at each end or slightly tapering anteriorly; chorion sculptured, either with distinct longitudinal ridges, some anastomosing, or with more reticulated pattern of ridges; with small depressed micropylar opening anteriorly; posteriorly with small pad with several large pores of unknown function.

Larvae (Figs 72, 73; Chapter 13, fig. 156) musciform, tapering anteriorly and rather blunt posteriorly, usually somewhat dorsoventrally compressed, with conspicuous secondary annulations dorsally, each appearing as 3 pseudosegments clothed in small chaetoids (rarely smooth); middle pseudosegment usually with transverse row of enlarged chaetoids or fleshy spines; usually with lateral and ventral creeping welts; prothoracic spiracles protruding laterally, arranged fanwise (Fig. 76), with 3–12 papillae; posterior spiracles usually on distinctly separated divergent stalks (flattened in *Leucopomyia* Malloch), each (Fig. 77; Chapter 13, fig. 158) with 3 papillae, bearing 1 opening each; first-instar larvae with only 2 such lobes on each short stalk; cephaloskeleton (Figs 78–81; Chapter 13, fig. 157) simple and slender; mouthhook simple and curved, dental sclerite usually absent, intermediate and basal sclerites separate (Figs 78–80) or fused (Chapter 13, fig. 157), parastomal bar absent, with long slender cornua; gular region sometimes with cephalic ring (Fig. 81).

Puparium (Figs 74, 75) subovate, anterior end abruptly tapered; usually slightly dorsoventrally compressed, more or less convex dorsally and flattened ventrally; anterior end usually dorsoventrally flattened to produce lateral ridge; surface sculpturing and creeping welts reflect third-instar larval conditions, but more flattened; prothoracic and posterior spiracles as in third-instar larva; usually with hardened shiny black droplet present posteriorly (Fig. 75), excreted at pupariation.

Families superficially similar to Chamaemyiidae, *i.e.*, small grey or black acalyptrates, such as some Agromyzidae (see Chapter 86), Canacidae (see Chapter 94), Chloropidae (see Chapter 96), Ephydridae (see Chapter 100), Heleomyzidae (see Chapter 98) and Odiniidae (see Chapter 83), can be readily separated from these by the following suite of chamaemyiid characteristics: 0–2 reclinate fronto-orbital setae; vibrissa absent; postocellar setae convergent or absent; costal wing vein (*C*) unbroken; subcostal vein (*Sc*) complete, separated from vein R_1; presence of a prescutellum and lack of preapical dorsal tibial setae. Chamaemyiids can be separated from the most similar family, the closely related Lauxaniidae, on the basis of the developed prescutellum, the lack of distinct dense black costal spinules, the absence of preapical dorsal tibial setae and in some genera the lack of fronto-orbital and/or anepisternal setae.

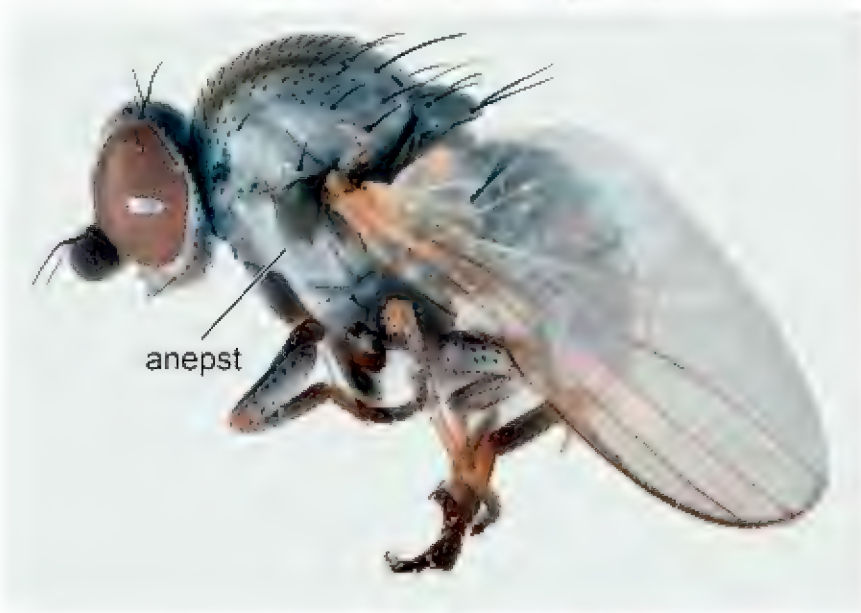
Biology and immature stages

The representatives of the family with known biology are predators on sternorrhynchous Hemiptera, particularly aphidoid or coccoid. Specific biological data are known for about half the described species of Afrotropical chamaemyiids, in addition to those species that had been introduced from other regions. Overall, there is a reasonable understanding of trends in chamaemyiid biology and predatory habits appear relatively uniform at the genus-group level (Gaimari 2010: 1000). As a whole, they display a spectrum of feeding strategies, from active predation within free-living prey colonies to completely sessile predation on eggs within a single coccoid egg-sac. The following are several more or less genus-specific feeding strategies, focusing on those genera present in the Afrotropical Region, regardless of whether the records are for Afrotropical species: mealybugs in leaf sheaths of grasses are attacked by species of *Chamaemyia* Meigen (Raspi 1983; Sluss & Foote 1973; Tanasijtshuk 1970) and *Parochthiphila* Czerny (Raspi 1983; Tanasijtshuk 1963, 1968); adelgids on gymnosperms are attacked by species of *Neoleucopis* Malloch (Clark & Brown 1957; McAlpine 1971; Sluss & Foote 1973), with some species attacking margarodid scales on gymnosperms (Gaimari *et al.* 2007); scales and mealybugs on dicots are attacked by species of *Leucopis* Meigen, subgenus *Leucopella* Malloch (Gaimari & Raspi 2002; James 1934; Malloch 1927); on eggs within ovisacs of coccoids by species of *Leucopomyia* (Kaydan *et al.* 2006; Malloch 1922; Raspi & Bertolini 1993; Tanasijtshuk 1986: 191) and Undescribed genus A. Some, such as *Leucopis sensu stricto*, have broader feeding strategies, feeding on almost the entire range of available prey above and adding aphids on gymnosperms, grasses and dicots. Species in some genera feed in tight enclosures where other predators cannot typically enter, including feeding on mealybugs or aphids in the leaf sheaths of grasses (Gaimari & Turner 1996*a*, 1998), within aphidoid galls (Raspi 1990; Stevenson 1967; Valenti & Gaimari 1992; Valenti *et al.* 1996), within root systems infested with aphids or mealybugs and within the dense waxy substrates of various aphidoid and coccoid colonies.

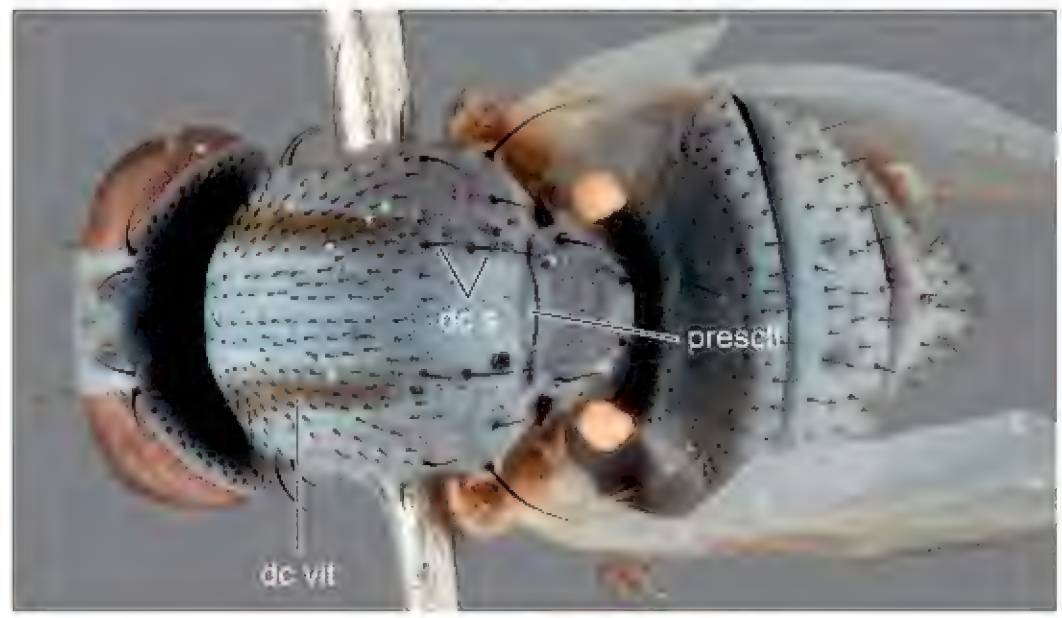
Focusing on the Afrotropical fauna, the known hosts for the described *Leucopis* (*Leucopella*) include nine species in seven genera of Pseudococcidae (*Maconellicoccus* Ezzat, *Nipaecoccus* Šulc, *Paracoccus* Ezzat & McConnell, *Planococcus*

8 *Leucopis* (*Leucopella*) ♂

9 *Leucopis* (*Leucopella*) ♂



10 *Leucopis* (*Leucopis*) ♂



11 *Leucopis* (*Leucopis*) ♂

12 *Leucopomyia* ♀

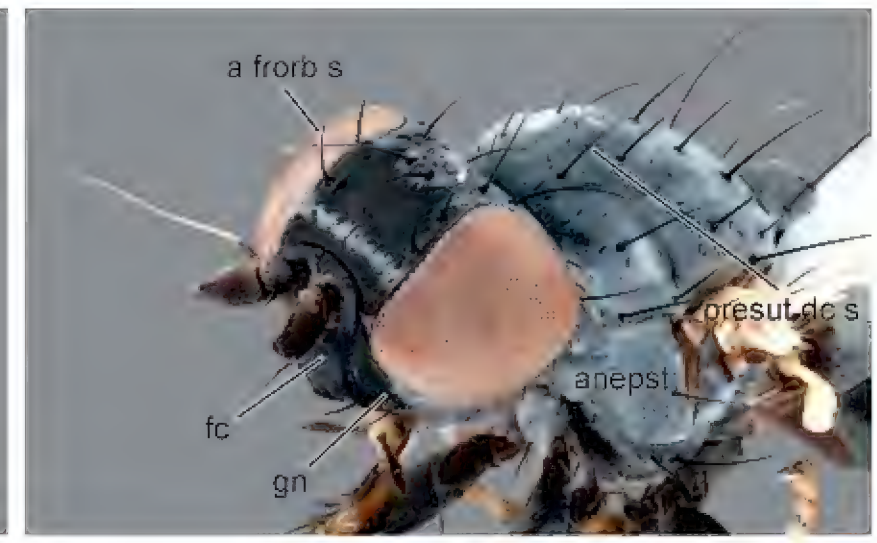
13 *Leucopomyia* ♀

Figs 76.8–13. Habitus and heads and thoraces of Chamaemyiidae: (8) habitus of *Leucopis* (*Leucopella*) sp., lateral view ♂; (9) same, head and thorax, dorsolateral oblique view; (10) habitus of *Leucopis* (*Leucopis*) sp., lateral view ♂; (11) same, dorsal view; (12) habitus of *Leucopomyia* sp., lateral view ♀; (13) same, head and thorax dorsal view.

Abbreviations: anepst – anepisternum; anepst s – anepisternal seta; dc s – dorsocentral setae; dc vit – dorsocentral vitta; oc s – ocellar setae; presctl – prescutellum; presctl acr s – prescutellar acrostichal seta.

Ferris, *Pseudococcus* Westwood, *Rastrococcus* Ferris and *Spilococcus* Ferris), five species in four genera of Coccidae (*Ceronema* Maskell, *Parasaissetia* Takahashi, *Pulvinaria* Targioni Tozetti and *Saissetia* Deplanche) and one species of Margarodidae (*Icerya purchasi* Maskell), in all attacking at least 14 plant species (including economically important plants, such as citrus, coffee and mango) in eight families – Anacardiaceae, Annonaceae, Apocynaceae, Euphorbiaceae, Fabaceae, Rubiaceae,

14 *Melanochthiphila* ♀

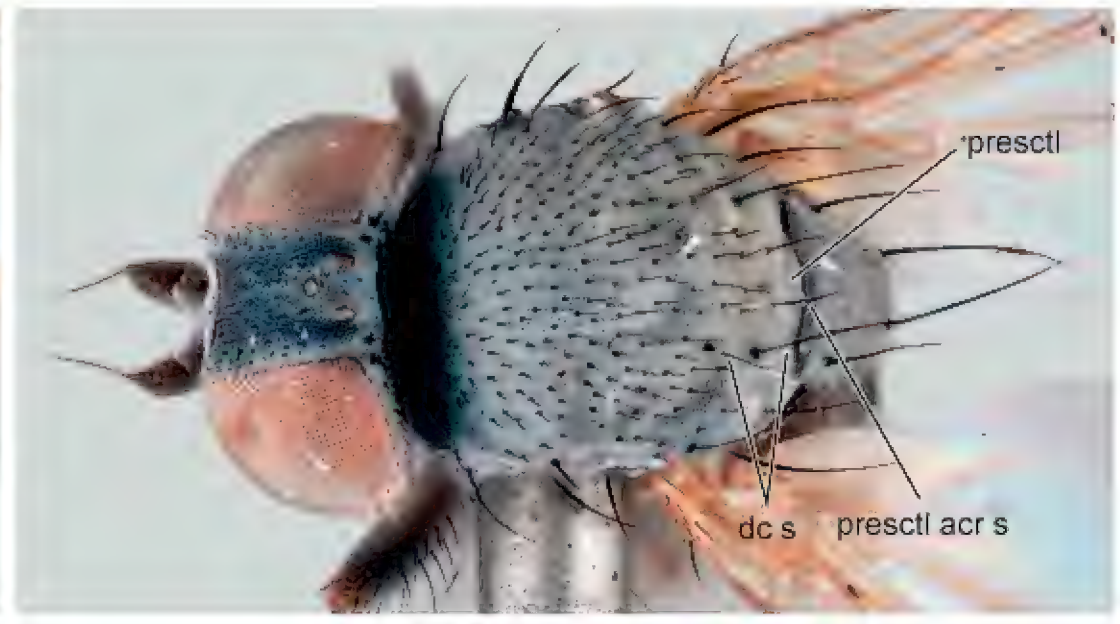


15 *Melanochthiphila* ♀

16 *Melanochthiphila* ♂

17 *Melanochthiphila* ♂

18 *Neoleucopis* ♀



19 *Neoleucopis* ♀

Figs 76.14–19. Habitus and heads and thoraces of Chamaemyiidae: (14) habitus of *Melanochthiphila* sp., lateral view ♀; (15) same, head and thorax, dorsolateral oblique view; (16) habitus of *Melanochthiphila* sp., lateral view ♂; (17) same, head and thorax, dorsolateral oblique view; (18) habitus of *Neoleucopis atratula* (Ratzeburg), lateral view ♀; (19) same, head and thorax, dorsal view.

Abbreviations: a frorb s – anterior fronto-orbital seta; anepst – anepisternum; dc s – dorsocentral setae; fc – face; gn – gena; presctl – prescutellum; presctl acr s – prescutellar acrostichal seta; presut dc s – presutural dorsocentral seta.

Rutaceae, Sapindaceae (Gaimari & Raspi 2002). For Undescribed genus A, the one species is known to feed on the eggs of three species of Coccidae in the genera *Ceroplastes* Gray, *Parasaissetia* and *Saissetia*, with the first named on *Euclea diviniana* Hiern (Ebenaceae) and the last two named on *Warburgia ugandensis* Sprague (Canellaceae). For *Parochthiphila*, although the host list is likely very extensive for this genus, the writer has only reared one undescribed Afrotropical species feeding on a species of mealybug, *Brevennia* Goux (Pseudococcidae) on Poaceae in South Africa.

Beyond host records, larval and adult behaviour is poorly known. McLean (1992) made observations on larval feeding on aphids and their being ignored by the ants tending the aphids, and on the adults approaching an aphid colony to oviposit and their avoidance of ants. Additionally, the adults are known to stroke the aphids with their fore tarsi to elicit honeydew secretion (presumably mimicking the ants' antennal actions for the same purpose), which is fed upon by the adult flies. Gaimari & Turner (1998) made observations of larval searching and feeding behaviour by instar, moulting and pupariation, adult courtship behaviour (including wing fluttering, wing extension, body postures and touching) and oviposition. Benelli *et al*. (2014) were the first to perform quantitative studies of courtship behaviour for one species of *Leucopis*, assessing visual, olfactory and tactile cues. At least one Nearctic species was reported to use dietary-acquired carminic acid (the red dye from cochineal bugs) for defence, with the liquid stored in a special rectal pouch and in the Malpighian tubules and expressed from the rectum in response to molestation by ants (Eisner *et al*. 1994). In at least some species, just prior to pupariation, a sticky liquid is secreted from the anus, likely from the Malpighian tubules, which is spread over the entire ventral surface of the larva and hardens after pupariation, adhering the puparium to the substrate; after this secretion, the gut purges a thin, sticky black fluid that hardens to form a characteristic

20 *Parochthiphila* (*Euestelia*) ♂

21 *Parochthiphila* (*Euestelia*) ♂

22 *Parochthiphila* (*Parochthiphila*) ♂

23 *Parochthiphila* (*Parochthiphila*) ♂

Figs 76.20–23. Habitus and heads and thoraces of Chamaemyiidae: (20) habitus of *Parochthiphila* (*Euestelia*) sp., lateral view ♂; (21) same, head and thorax, dorsolateral oblique view; (22) habitus of *Parochthiphila* (*Parochthiphila*) sp., lateral view ♂; (23) same, head and thorax, dorsolateral oblique view.

Abbreviations: a frorb s – anterior fronto-orbital seta; anepst – anepisternum; anepst s – anepisternal seta; fr – frons; presut dc s – presutural dorsocentral seta.

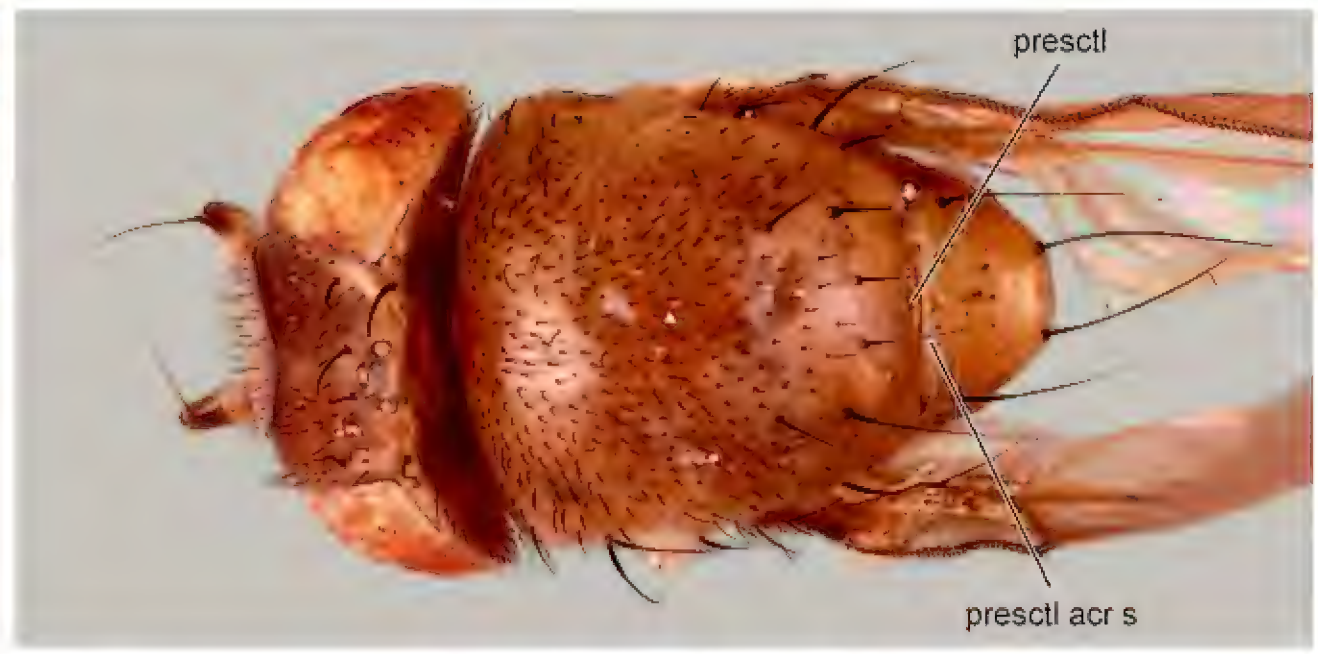
shiny black droplet attached to the posterior end of the puparium (Gaimari & Turner 1998).

Morphology of the known immature stages in the family is summarised in part by Ferrar (1987: 103, 608), and supplemented by Foote (1991: 835), McAlpine (1987: 966) and Gaimari (2010: 998), and although the immatures remain undescribed for any Afrotropical species, details and extensive figures are provided for all stages and instars for species representing several genera that do occur in the Afrotropics, including: *Chamaemyia* (Raspi 1983; Sluss & Foote 1973), *Leucopis sensu stricto* (Gaimari & Turner 1996*b*; Raspi 1983, 1990), *Neoleucopis* (Gaimari *et al*. 2007; Sluss & Foote 1973) and *Parochthiphila* (Raspi 1983). Eggs are discussed generally by Tanasijtshuk (1974) for several genera, all of which occur in the Afrotropics, including *Acrometopia* Schiner, *Chamaemyia*, *Leucopis sensu stricto* and *Parochthiphila*, noting some fundamental differences in surface sculpturing among genera. Mazzini & Raspi (1983) provided extensive figures and descriptions of eggs for species of *Chamaemyia* and *Parochthiphila*. Larvae and puparia have also been figured and discussed briefly in various revisionary studies.

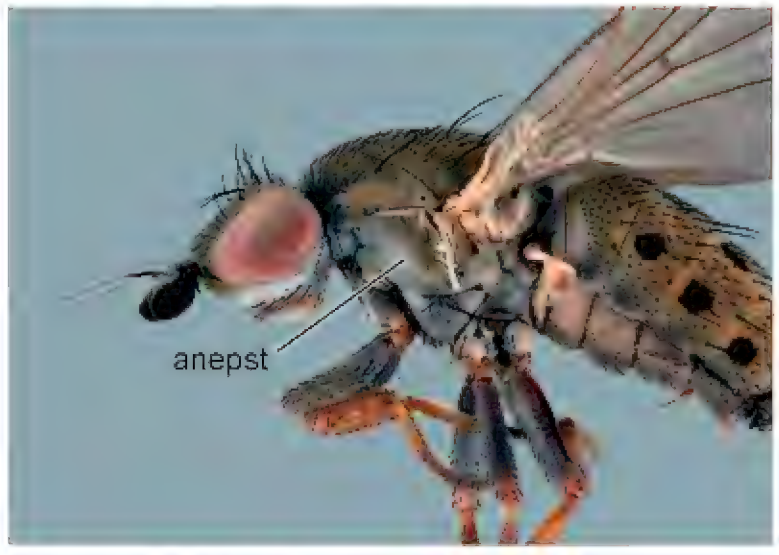
Economic significance

Given the predaceous habits of the larvae of Chamaemyiidae on aphidoid and coccoid Hemiptera, they are among the suite of enemies that can affect populations of these plant-sucking insects, some of which can be important pests. Various species, solely in the Leucopini, have been introduced as biological control agents targeting particular pest species, although only a small number have been released in the Afrotropics. Among the releases for biological control, many have occurred in North America, which include species attacking Russian wheat aphid, *Diuraphis noxia* (Mordvilko) (Gaimari & Turner 1996*b*; Noma *et al*. 2005; Olfert *et al*. 2002: 110), other aphids (Barriault *et al*. 2019; Bellefeuille *et al*. 2019; Kaiser *et al*. 2007), and Balsam woolly adelgid, *Adelges piceae* (Ratzeburg) (Clark & Brown 1962; Clausen 1978: 50; McAlpine 1978; Ross *et al*. 2011: 98; Schooley *et al*. 1984: 231). The Hemlock woolly adelgid, *A. tsugae* Annand, is a more recent target for biological control efforts in North America (Ross *et al*. 2011: 99). Regarding *Diuraphis noxia* in the Afrotropics, the Palaearctic species *Leucopis ninae* Tanasijtshuk, 1966, was

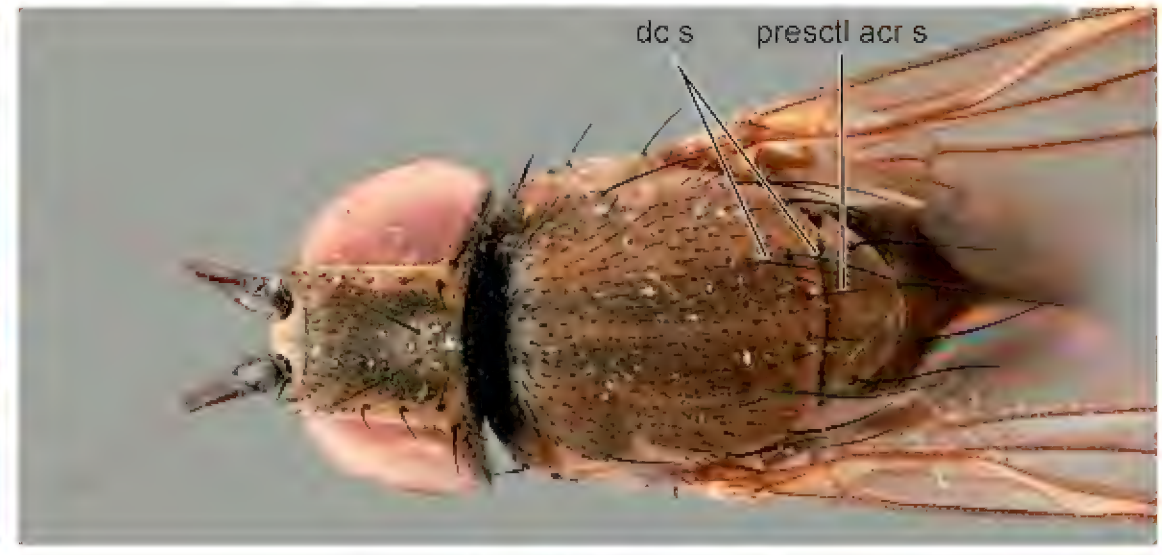
24 Undescribed genus A ♀



25 Undescribed genus A ♀



26 Undescribed genus B ♂



27 Undescribed genus B ♂

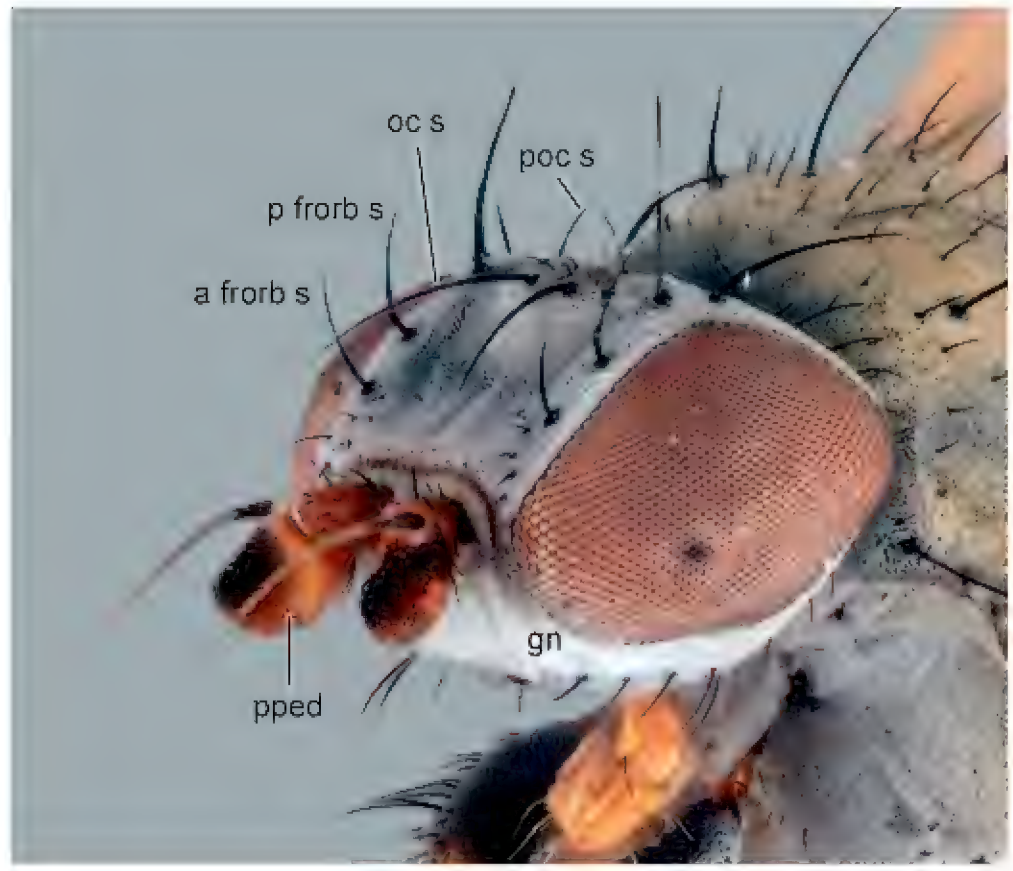
Figs 76.24–27. Habitus and heads and thoraces of Chamaemyiidae: (24) head and thorax of Undescribed genus A, lateral view ♀; (25) same, dorsal view; (26) habitus of Undescribed genus B, lateral view ♂; (27) same, head and thorax, dorsal view.

Abbreviations: anepst – anepisternum; dc s – dorsocentral setae; presctl – prescutellum; presctl acr s – prescutellar acrostichal seta.

released in at least South Africa (Tolmay & Prinsloo 1994) and although apparently established, its effectiveness has not been reported (Hatting 1995).

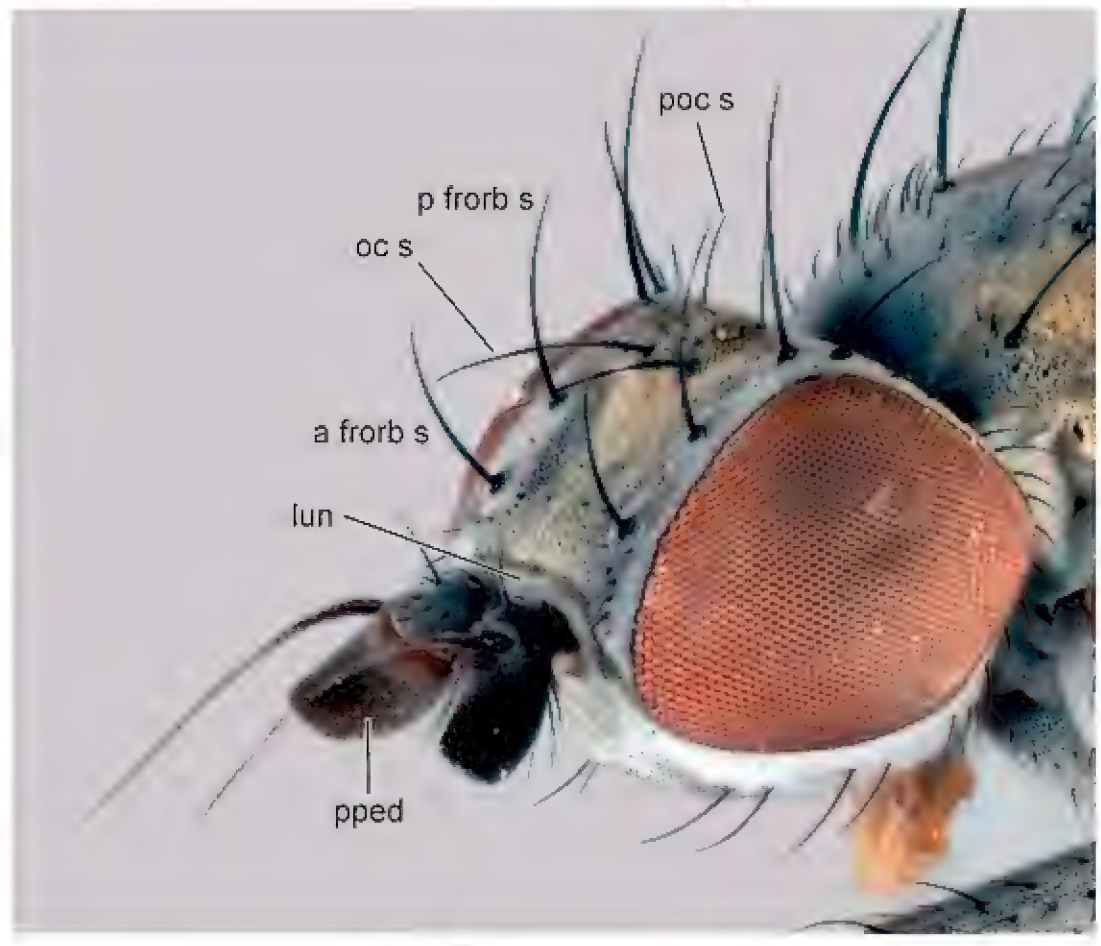
Outside of North America, the species of one adelgid species-complex have had considerable control effected on them by introduction of exotic chamaemyiids (Clausen 1978: 49; Mills 1990) – *Pineus pini* (Goeze) *sensu lato*. The taxonomy of this group is in need of revision, with various names applied to the different introductions into different parts of the world over time; the names involved include *Pineus boerneri* Annand, *P. laevis* (Maskell) and *P. pini* and no attempt was made here to differentiate them, due to the conflicting literature on the matter. The invasive introduction into Hawaii was well controlled

28 *Acrometopia* ♀



29 *Acrometopia* ♀

30 *Chamaemyia* ♂



31 *Chamaemyia* ♂

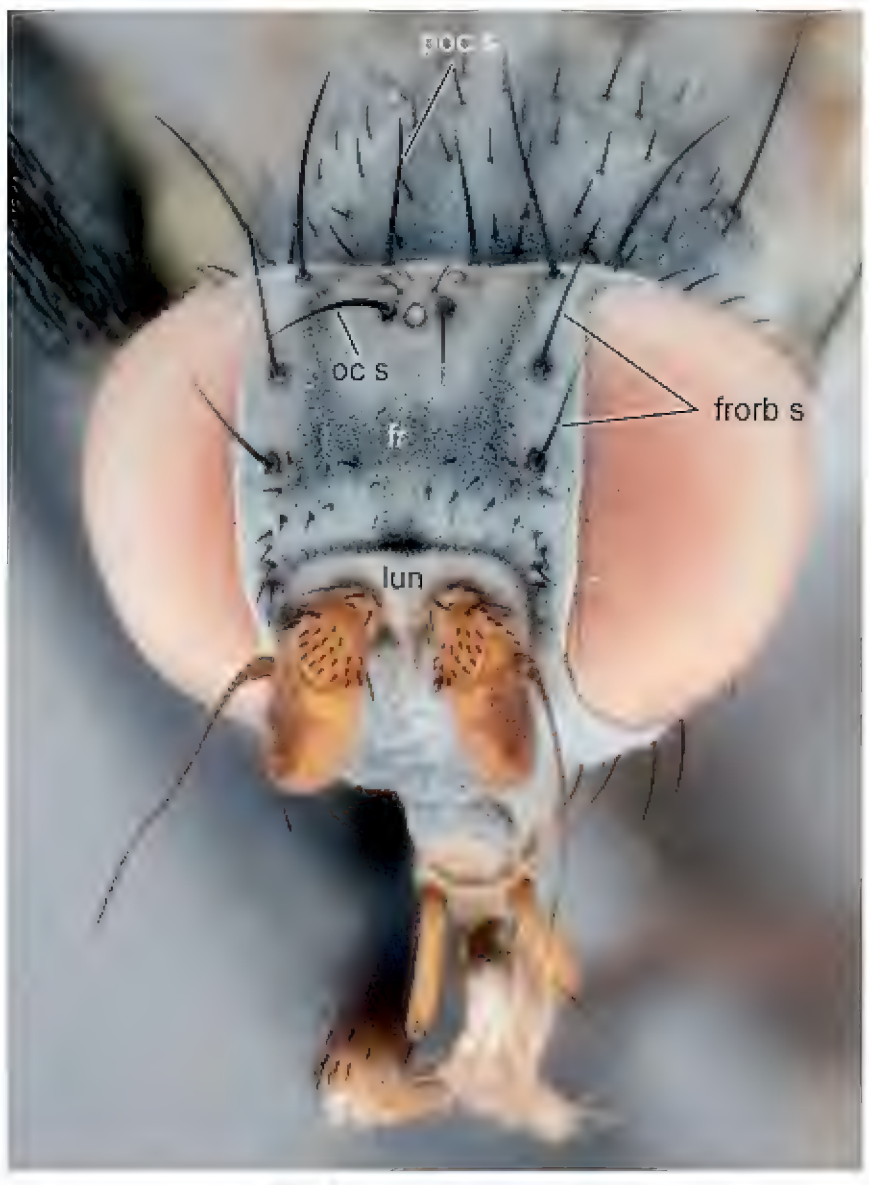
Figs 76.28–31. Heads of Chamaemyiidae: (28) *Acrometopia* sp., frontal view ♀; (29) same, lateral oblique view; (30) *Chamaemyia* sp., frontal view ♂; (31) same, lateral oblique view.

Abbreviations: a frorb s – anterior fronto-orbital seta; gn – gena; lun – lunule; oc s – ocellar seta; p frorb s – posterior fronto-orbital seta; poc s – postocellar seta; pped – postpedicel.

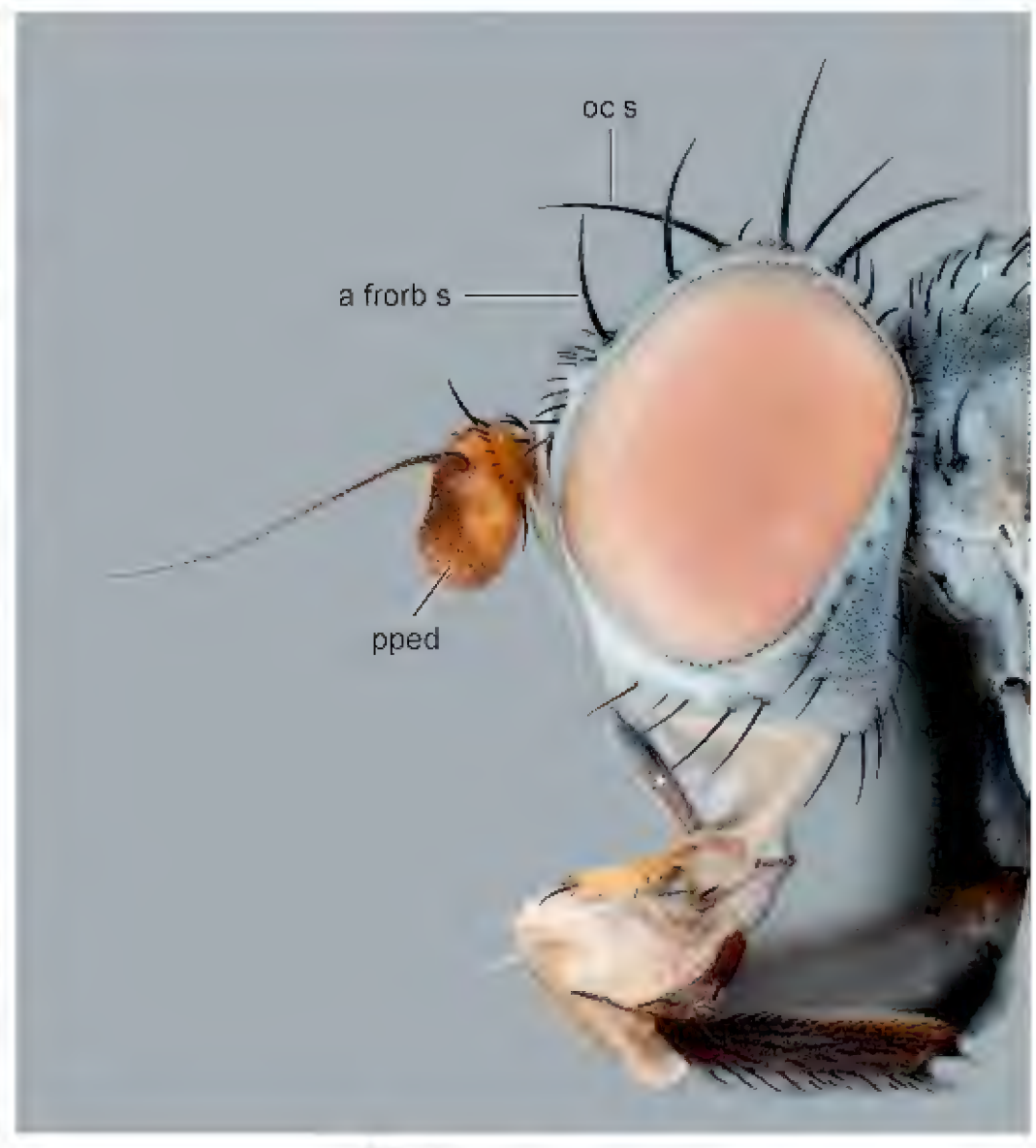
in the 1970s by introduction of *Neoleucopis tapiae* (Blanchard, 1964) (Culliney *et al*. 1988; Nakao *et al*. 1981), which had been misidentified as *N. obscura* (Haliday, 1833) (Greathead 1995); *N. nigraluna* (McAlpine, 1971) was also introduced and established, but its effectiveness has not been demonstrated. Introduced into New Zealand, the species was well controlled in the 1930s by introduction of *N. tapiae* (Zondag & Nuttall 1989) and in Chile in the 1940s by introduction of *N. obscura* (Zúñiga 1985), which may have been a misidentification, as the only species currently encountered in Chile is *N. tapiae*. In Australia, three species were released in the 1930s, *N. atratula* (Ratzeburg, 1844) (misidentified as *N. obscura*), *Lipoleucopis praecox* de Meijere, 1928 and *Leucopis atrifacies* Aldrich, 1925, with no known impact, although at least *N. atratula* is established (Tanasijtshuk 1996).

In the Afrotropics, the species accidentally introduced is generally thought to be *Pineus boerneri* (Blackman *et al*. 1995) and there have been considerable efforts made towards biocontrol of this pest (Day *et al*. 2003: 101). Among the species purposefully introduced in the 1970s, *Leucopis argenticollis* Zetterstedt, 1848, *Neoleucopis nigraluna* and *N. tapiae* and an unidentified species, only *N. tapiae* has become established. Oddly, *N. tapiae* was also found in Malawi and in South Africa, where it was thought to have been accidentally introduced on imported pines (Greathead 1995) and new specimens are now known from Burundi, suggesting it may also be present in Tanzania. Its effect on the pest species has not been determined.

Coccoids have seldom been the target for biological control efforts in various parts of the world. For example, the West Indian species *Melaleucopis simmondsi* Sabrosky, 1957, was released in the 1960s in Brazil against the ortheziid pest species *Insignorthezia insignis* (Browne, 1887), with no reports of establishment (Bartlett 1978: 136). In the Afrotropics, it was recognised quite early, even before the species was described (Kirkpatrick 1926), that the native species *Leucopis* (*Leucopella*) *africana* Malloch, 1927, was of potential importance in controlling pseudococcid pests of coffee, *Coffea arabica* L. (Rubiaceae), including *Planococcus citri* (Risso) (Malloch 1927), *Planococcus kenyae* (Le Pelley) (Oduor & Simons 2003: 351) and *Pseudococcus concavocerarii* James (James 1934). For *Rastrococcus iceryoides* (Green), two species, *L.* (*Leucopella*) *africana* and *L.* (*Leucopella*) *ardis* Gaimari & Raspi, 2002, are of potential biocontrol importance, because of the habit of the third-instar larva of tunnelling out of the ovisac, which exposes the eggs to adverse weather conditions, possibly inflicting greater mortality than the consumption of eggs itself (Chrysantus 2012).



32 *Hamecamyia* ♂



33 *Hamecamyia* ♂

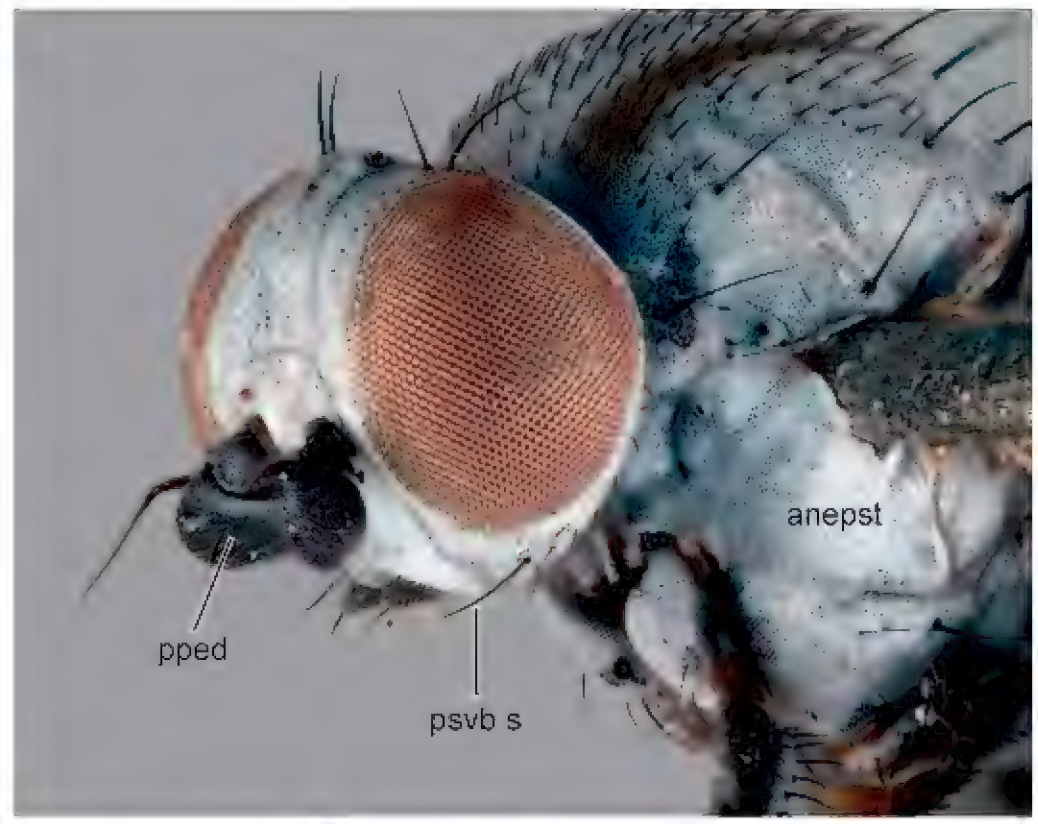
Figs 76.32–33. Heads of Chamaemyiidae: (32) *Hamecamyia stuckenbergi* Gaimari, frontal view ♂; (33) same, lateral view. Figs 32, 33 (Gaimari 2012, figs 3, 4).

Abbreviations: a frorb s – anterior fronto-orbital seta; fr – frons; frorb s – fronto-orbital setae; lun – lunule; oc s – ocellar seta; poc s – postocellar seta; pped – postpedicel.

Classification

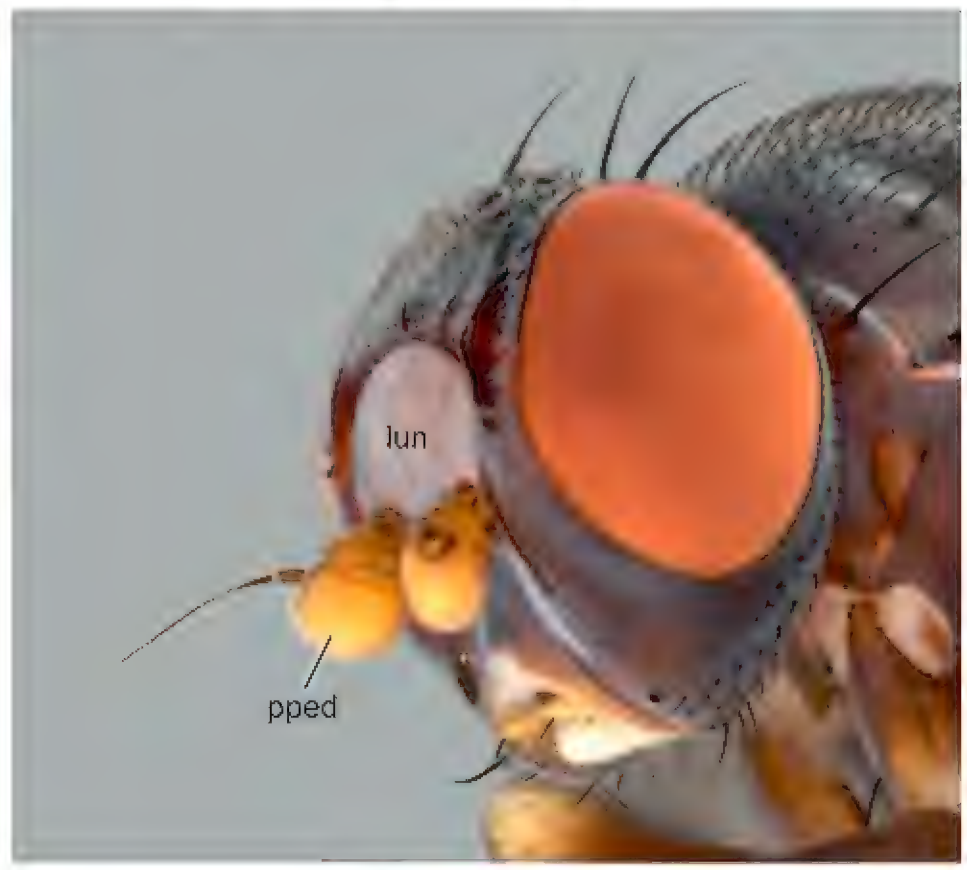
The classification of Chamaemyiidae is discussed in Gaimari (2010: 1001), which is reiterated here, with some additional focus on Afrotropical taxa. The family-group was first named by Fallén (1823: 8), as Ochtidiae (for his genus *Ochtiphila* Fallén, which was subsequently synonymised under *Chamaemyia*). As such, the family-group name Chamaemyiinae was adopted by Hendel (1910), noting the priority of *Chamaemyia* over *Ochtiphila*. This group was later treated by Malloch (1922) as a subfamily of Agromyzidae (as Ochthiphilinae, based on the misspelling *Ochthiphila* by Meigen (1830: 90)), a position he later (Malloch 1930) abandoned, to follow Hendel (1916) in allying the family with Lauxaniidae. McAlpine (1963) divided the family into two subfamilies, Chamaemyiinae and Cremifaniinae, which was strongly endorsed by Hennig (1965) and McAlpine (1989: 1448) cited at least 10 synapomorphic character states supporting the monophyly of the family to include Cremifaniinae, including larval predation on sternorrhynchous hemipterans, fusion of the larval intermediate and basal sclerites and the parastomal bar with the intermediate sclerites of the cephaloskeleton, presence of unbranched peristigmatic

34 *Leucopis* (*Leucopis*) ♂



35 *Leucopis* (*Leucopis*) ♂

36 *Leucopomyia* ♀



37 *Leucopomyia* ♀

Figs 76.34–37. Heads of Chamaemyiidae: (34) *Leucopis* (*Leucopis*) sp., frontal view ♂; (35) same, lateral oblique view; (36) *Leucopomyia* sp., frontal view ♀; (37) same (but different species), lateral oblique view.

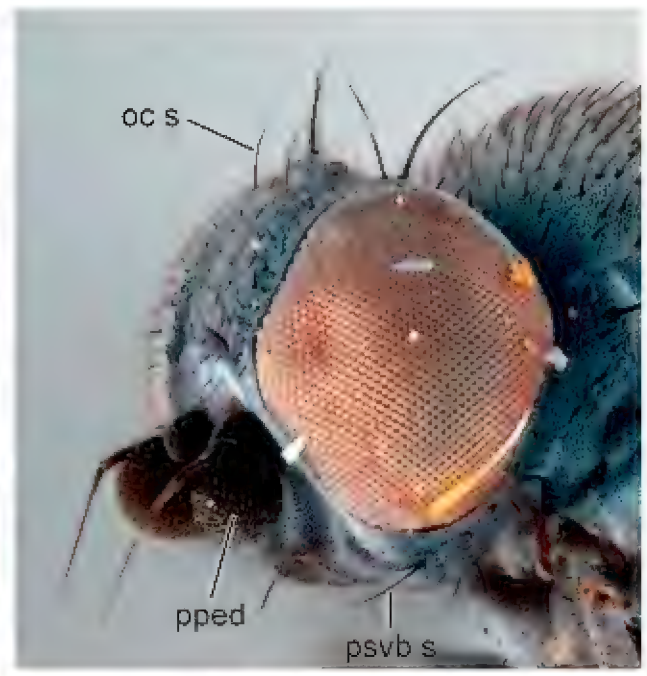
Abbreviations: anepst – anepisternum; fr – frons; lun – lunule; pped – postpedicel; psvb s – pseudovibrissal seta.

tufts on the posterior spiracles, a bare adult prosternum, absence of a proanepimeral seta, flexion of wing vein R_1 towards the apical bend of the subcostal vein (*Sc*), absence of a preapical dorsal tibial seta, presence of heavily grey pruinose body vestiture and the length of tergite 6 in males being less than half that of tergite 5.

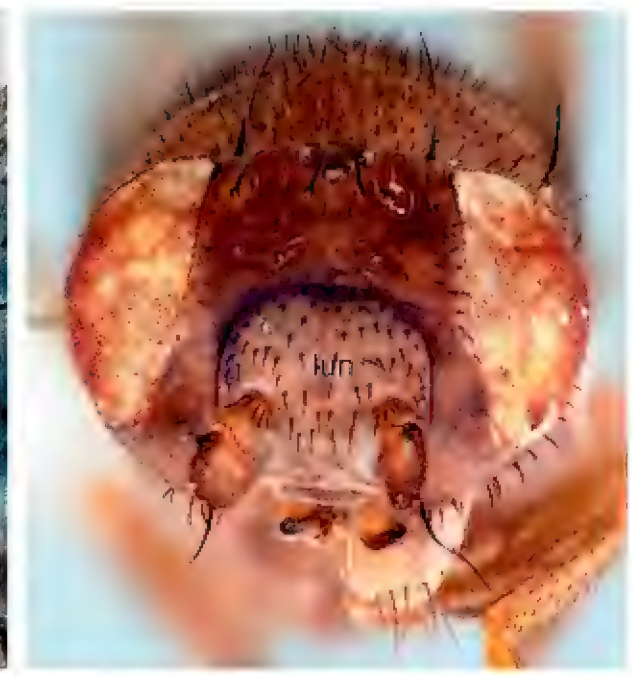
Griffiths (1972: 187) disagreed with the initial assessment of McAlpine (1963), and treated Cremifaniinae at the family-level, as an unplaced representative of the Sciomyzoidea, separated from the Lauxanioidea by the asymmetry of male abdominal segments 6–8 and the articulated phallic sclerites, that allow swinging through a wide arc against the phallapodeme to reach a more anteriorly directed position. Griffiths' (1972) opinion was later followed by Tanasijtshuk (1984, 1992), although McAlpine (1989: 1449) pointed to several misinterpretations by Griffiths, including, for example, the complex phallic structure found in many lauxaniids functioning similarly to *Cremifania* Czerny, allowing for the possibility that this sort of arcing phallus could be in the lauxanioid groundplan, which was secondarily changed (an autapomorphy) in his Chamaemyiinae and some lauxaniids. The same can be said for the presence of three spermathecae (1 + 2) in *Cremifania*, a characteristic seemingly in opposition to the four spermathecae (2 + 2) typically cited in other chamaemyiids (Papp 1998: 411). Not only is this condition consistent with the groundplan of Lauxanioidea, but at least one chamaemyiid genus has been found with variable states in spermathecal number, due to fusion of one or both pairs (Gaimari & Tanasijtshuk 2001), so this characteristic provides no definitive data to contradict the placement of *Cremifania* within the family.

In McAlpine's (1963, 1989: 1449) scheme, which is followed herein, Chamaemyiinae are supported by four autapomorphies, including the lack of discrete surstyli on the epandrium, fusion of the phallapodeme to the hypandrium and uniform sclerotisation of the phallus into a rigid and posteroventrally directed structure. Chamaemyiinae are divided into two tribes, Chamaemyiini and Leucopini, with Chamaemyiini weakly supported by the reduction of the pregonite and Leucopini more strongly supported by the lunule being broadly exposed, the absence of postocellar setae, reduction or absence of fronto-orbital setae,

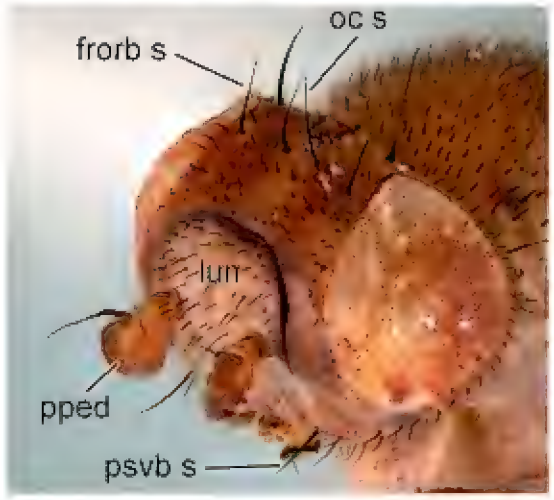
38 *Neoleucopis* ♀



39 *Neoleucopis* ♀

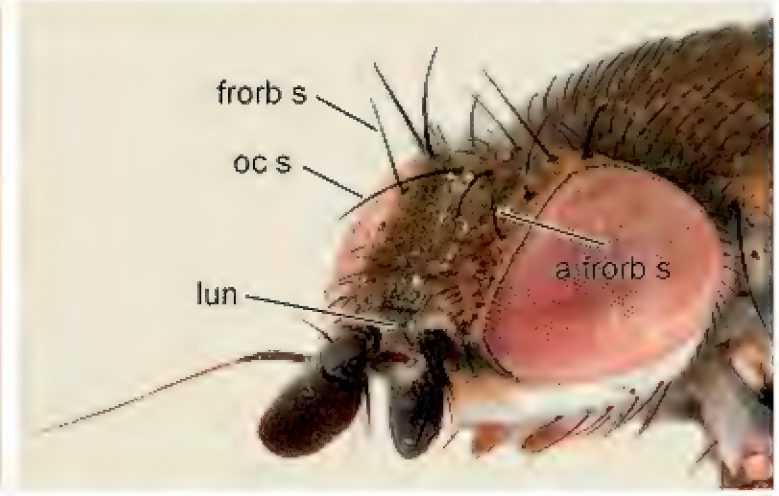


40 Undescribed genus A ♀



41 Undescribed genus A ♀

42 Undescribed genus B ♂



43 Undescribed genus B ♂

Figs 76.38–43. Heads of Chamaemyiidae: (38) *Neoleucopis atratula* (Ratzeburg), frontal view ♀; (39) same, lateral oblique view; (40) Undescribed genus A, frontal view ♀; (41) same, dorsolateral oblique view; (42) Undescribed genus B, frontal view ♂; (43) same, lateral oblique view.

Abbreviations: a frorb s – anterior fronto-orbital seta; fr – frons; frorb s – fronto-orbital seta; lun – lunule; oc s – ocellar seta; pped – postpedicel; psvb s – pseudovibrissal seta.

the atrophied wing vein *CuA+CuP* and tergite 6 in males being lost or fused with syntergosternite 7 + 8.

Relationships among chamaemyiid genera have been considered by Tanasijtshuk (1986: 71, 1992, 2003). In considering relationships among 16 (Tanasijtshuk 1992) and 22 (Tanasijtshuk 2003) chamaemyiid genera, a hierarchical classification was proposed with two subfamilies, Chamaemyiinae and Leucopinae, which were elevations in rank for the tribes recognised by McAlpine (1963) after exclusion of Cremifaniinae. In the current scheme recognising Cremifaniinae and Chamaemyiinae as the two subfamilies of Chamaemyiidae (Gaimari 2010: 1001), the tribal divisions of Chamaemyiinae are Chamaemyiini and Leucopini.

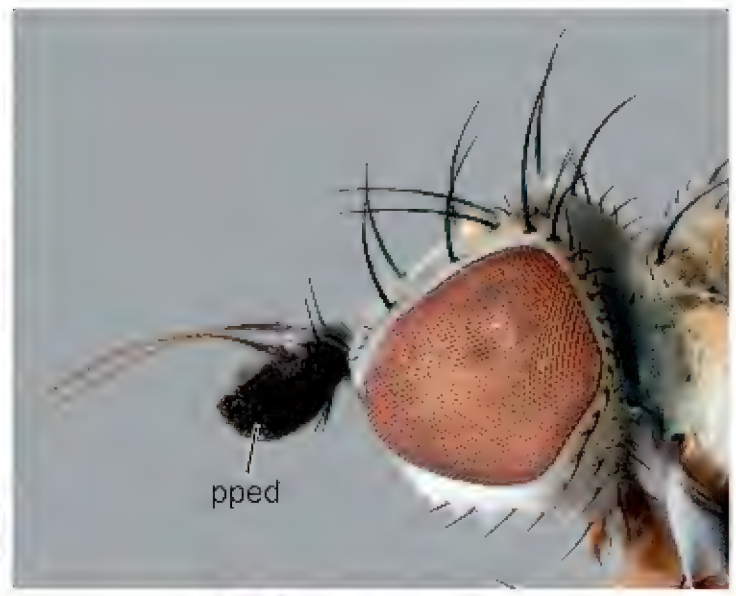
Chamaemyiini is divided into three subtribes, two of which occur in the Afrotropical Region: Acrometopiina (including *Acrometopia*, *Melanochthiphila* Frey and *Parochthiphila* in the Afrotropics), Chamaemyiina (including only *Chamaemyia* in the Afrotropics) and Pseudoleucopina (non-Afrotropical). The genera *Hamecamyia* Gaimari and Undescribed genus B are also both in Chamaemyiini, with the former very likely in the Acrometopiina, given the posited close relationship of the genus with *Parochthiphila* (Gaimari 2012). Leucopini contains the following genera present in the Afrotropics: *Leucopis* (including subgenera *L.* (*Leucopella*) and *Leucopis sensu stricto*), *Leucopomyia*, *Lipoleucopis*, *Neoleucopis* and Undescribed genus A. There are no Cremifaniinae in the Afrotropical Region.

Only a single fossil species, *Procremifania electrica* Hennig, 1965, a representative of the subfamily Cremifaniinae, has been described from Baltic amber. No other fossil chamaemyiids are known, although Poinar (1992: 286) reported the family in his list of families reported from Dominican amber.

Identification

Identification keys to genera are available for the Nearctic Region (McAlpine 1987: 966), which was updated and expanded for the New World (Gaimari 2010: 1002), and the Palaearctic Region (McLean 1998: 421), although Cremifaniinae was treated as a separate family in the regional manual by Papp (1998: 409). The resources for the Palaearctic Region

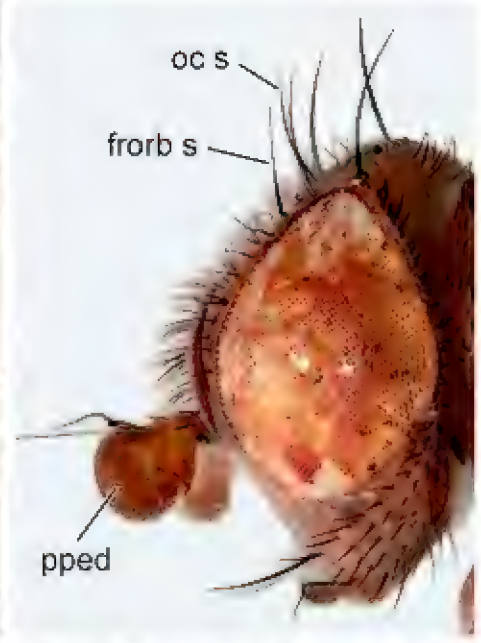
44 *Acrometopia* ♀



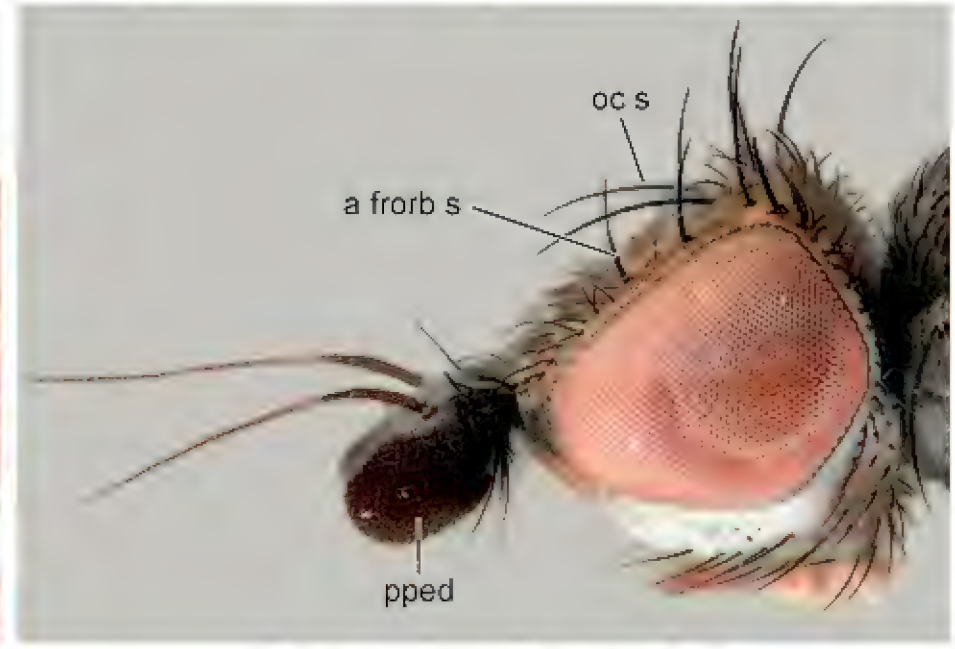
45 *Chamaemyia* ♂

46 *Leucopis* (*Leucopis*) ♂

47 *Leucopomyia* ♀



48 Undescribed genus A ♀

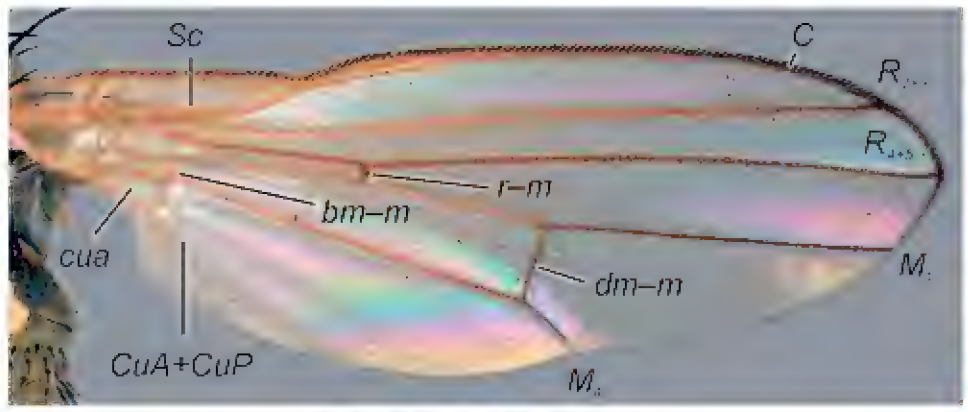


49 Undescribed genus B ♂

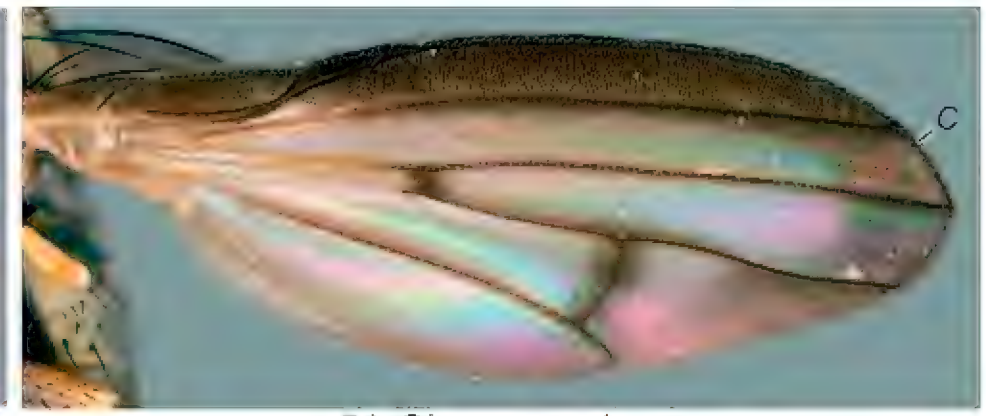
Figs 76.44–49. Heads of Chamaemyiidae (lateral views): (44) *Acrometopia* sp. ♀; (45) *Chamaemyia* sp. ♂; (46) *Leucopis* (*Leucopis*) sp. ♂; (47) *Leucopomyia* sp. ♀; (48) Undescribed genus A ♀; (49) Undescribed genus B ♂.

Abbreviations: a frorb s – anterior fronto-orbital seta; frorb s – fronto-orbital seta; oc s – ocellar seta; pped – postpedicel.

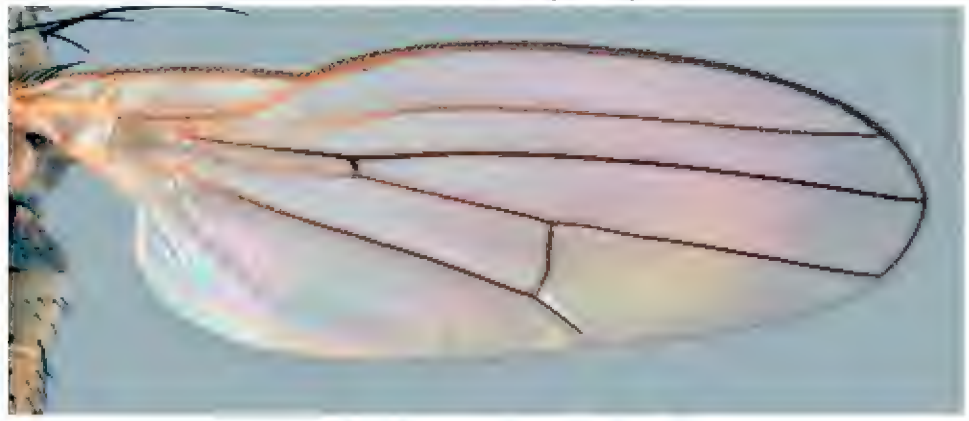
are most complete, with much of the fauna revised by Tanasijtshuk (1986: 86). For the Australian fauna, Tanasijtshuk (1996) provides descriptions and identification keys to genera and species, but many undescribed species remain. Resources to identify Afrotropical chamaemyiids are sparse and only eight species are listed in the most recent catalogue (Cogan 1980: 601), at least three of which are either invalid or were based on misidentifications. Only *Leucopis* (*Leucopella*) was



50 *Acrometopia* ♀



51 *Chamaemyia* ♂

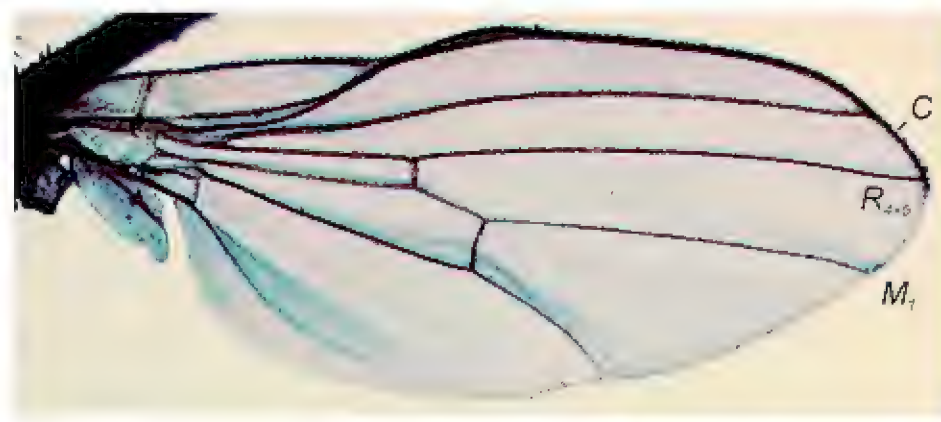


52 *Chamaemyia* ♂

53 *Hamecamyia* ♂

54 *Leucopis* (*Leucopis*) ♂

55 *Leucopomyia* ♀



56 *Lipoleucopis* ♂

Figs 76.50–56. Wings of Chamaemyiidae (dorsal views): (50) *Acrometopia* sp. ♀; (51) *Chamaemyia* sp. ♂; (52) *Chamaemyia* sp. ♂; (53) *Hamecamyia stuckenbergi* Gaimari ♂; (54) *Leucopis* (*Leucopis*) sp. ♂; (55) *Leucopomyia* sp. ♀; (56) *Lipoleucopis praecox* de Meijere ♂ (non-Afrotropical). Fig. 53 (Gaimari 2012, fig. 7).

Abbreviations: *bm–m* – basal medial crossvein; *C* – costal vein; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *dm–m* – discal medial crossvein; M_1 – first branch of media; M_4 – fourth branch of media; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Sc* – subcostal vein.

revised recently, with identification keys to species (Gaimari & Raspi 2002), although only the fauna of north-eastern Africa was covered. Of the remaining genera most are currently monotypic, but with recognised greater diversity. Until these genera are revised, identifying the known species remains problematic, relying entirely on the isolated descriptions of species. Chamaemyiidae are best micro-pinned in the field for later double-mounting (see Chapter 2).

Key to genera of Afrotropical Chamaemyiidae

1. Body stout, with thorax and abdomen subequal in length (e.g., Figs 8, 10, 12, 18); head with lunule high, arched (e.g., Figs 34, 36, 38, 40), sometimes setulose (Figs 38, 40); without postocellar setae (e.g., Figs 34–36); without ocellar setae (e.g., Figs 35, 37), or these small and reclinate (e.g., Figs 39, 41); without fronto-orbital setae (e.g., Figs 35, 37, 46, 47), or with only 1 present (e.g., Figs 41, 48) (LEUCOPINI) 2

– Body elongate, with abdomen longer than thorax (e.g., Figs 2, 4, 6, 14, 16, 20, 22, 26); head with lunule narrow, bare (e.g., Figs 28, 30, 32); with postocellar setae (e.g., Figs 28, 30, 32); ocellar setae long, proclinate (e.g., Figs 29, 31, 43); with 2 strong fronto-orbital setae (e.g., Figs 29, 31, 49) (CHAMAEMYIINI) 7

2. Thorax without prescutellum; costal wing vein (C) ending at vein R_{4+5} (Fig. 56). . . . . *Lipoleucopis* de Meijere

– Thorax with prescutellum (e.g., Figs 1, 11, 13, 19, 25); costal wing vein (C) ending at vein M_1 (e.g., Figs 54, 55). 3

3. Thorax with anepisternum with 1 to several setae or setulae, or both, along posterior or lower margin (Figs 8, 9) . . . . . *Leucopis* (*Leucopella* Malloch)

– Thorax with anepisternum bare, lacking setae or setulae (e.g., Figs 10, 12, 24, 35) 4

4. Head with lunule and frons heavily setulose, with setulae as strong as those on mesonotum (Fig. 41); with ocellar setae, reclinate, nearly as strong as outer vertical seta (Fig. 41, but note outer vertical seta is broken-off, but is *ca* same size as fronto-orbital seta); with fronto-orbital seta on upper ½ of frons, nearly as strong as ocellar seta (Figs 41, 48). . . . . Undescribed genus A

– Head with lunule and frons setulose or bare (e.g., Figs 34, 36, 38), if setulose, then setulae usually much weaker than those on mesonotum (e.g., Fig. 39); without ocellar setae (e.g., Figs 34, 35, 37), or these very small (½ length of outer vertical seta) (e.g., Fig. 39); without fronto-orbital setae (e.g., Figs 34, 35, 37, 39). 5

5. Head with short ocellar setae (Fig. 39); thorax without dorsocentral vittae (Fig. 19); with prescutellar acrostichal setae (Fig. 19); abdominal tergite 3 without paired maculae (Fig. 62) . . . . . *Neoleucopis* Malloch

– Head without ocellar setae (e.g., Figs 35, 37); thorax usually with dorsocentral vittae, goldish or brownish (e.g., Figs 11, 13); with or without prescutellar acrostichal setae; at least abdominal tergite 3 usually with paired maculae (e.g., Figs 60, 61) 6

6. Thorax without prescutellar acrostichal setae (Fig. 11); without acrostichal setulae between posterior dorsocentral setae and prescutellum (except occasional stray setula) (Fig. 11); head length usually > ½ height (Fig. 46); lunule usually extended to only ⅓ distance from antennal base to anterior ocellus (Fig. 34). . . . . *Leucopis* (*Leucopis* Meigen)

– Thorax usually with prescutellar acrostichal setae; acrostichal setulae extending posteriorly to prescutellum, even if distinct prescutellar acrostichal setae absent (Fig. 13); head length ½ height or less (Fig. 47); lunule extending to ½ distance from antennal base to anterior ocellus (Fig. 36). . . . . *Leucopomyia* Malloch

7. Thorax with 2 dorsocentral setae, both postsutural, without presutural seta (e.g., Figs 7, 27) 8

– Thorax with 3 or more dorsocentral setae, almost invariably including strong presutural seta (e.g., Figs 3, 5, 15, 17, 21, 23). 9

8. Thorax without prescutellar acrostichal setae (Fig. 7); posterior dorsocentral seta equidistant between anterior seta and scutellar suture, or closer to suture (Fig. 7); head with anterior fronto-orbital seta inserted in anterior ½ of frons, closer to, or equidistant from, lunule than to posterior seta (Fig. 32) . . . . . *Hamecamyia* Gaimari

– Thorax with strong prescutellar acrostichal setae (Fig. 27); posterior dorsocentral seta closer to anterior seta than to scutellar suture (Fig. 27); head with fronto-orbital setae in posterior ½ of frons, with anterior seta closer to posterior seta than to lunule (Fig. 43, 49) . . . . . Undescribed genus B

9. Head with anterior fronto-orbital seta inserted far forward on frons, closer to lunule than to posterior seta (Fig. 31); thorax with dorsocentral setae 1 + 2, evenly spaced (Fig. 5); without anepisternal seta (Fig. 4); wing often darkened along costal vein (C) (Fig. 51), sometimes hyaline (Fig. 52) . . . . . *Chamaemyia* Meigen

– Head with anterior fronto-orbital seta inserted at least ⅓ frons length posterior to lunule, equidistant between posterior seta and lunule or closer to posterior seta (e.g., Figs 15, 17, 21, 23, 28, 29); thorax with dorsocentral setae 1 + 3 (e.g., Figs 15, 17, 23), or 1 + 2 with distinct gap where anteriormost postsutural seta would be if 1 + 3, sometimes with 1 or 2 reduced setae in gap (e.g., Figs 3, 21); anepisternal seta present or absent; wing hyaline, without markings (e.g., Fig. 50) 10

10. Overall appearance black (Fig. 16), with various areas lightly dusted with pruinescence (Figs 14, 15); always with glossy black face and adjacent part of gena (Fig. 15); thorax with anepisternal seta (Figs 14–17). . . . . *Melanochthiphila* Frey

– Overall appearance silvery grey to grey pruinose (e.g., Figs 2, 20, 22), including face and gena (e.g., Fig. 29); thorax with anepisternal seta present or absent. 11

11. Head longer than high, with face at least slightly receding (Fig. 44 illustrates receding angle from frons); eye elongate in horizontal axis (Figs 29, 44); frons never with black fascia between anterior fronto-orbital setae (Fig. 29); thorax without anepisternal seta (Fig. 2). . . . . *Acrometopia* Schiner

– Head higher than long or subequal, with face not receding (Figs 20, 22 illustrate obtuse angle from frons); eye elongate in vertical axis, or as high as long (Figs 20, 22); frons sometimes with black fascia between anterior fronto-orbital setae (Fig. 23); thorax with anepisternal seta present or absent . . . . . *Parochthiphila* Czerny 12

12. Thorax with anepisternal seta (Figs 22, 23) . . . . . *Parochthiphila sensu stricto*

– Thorax without anepisternal seta (Figs 20, 21) . . . . . *Parochthiphila* (*Euestelia* Enderlein)

Synopsis of the fauna

Although a small family with fewer than 350 species in 30 extant genera and subgenera, Chamaemyiidae have several widespread genera and subgenera. Most, however, are relatively restricted in their distribution. Only *Leucopis sensu stricto* is virtually cosmopolitan, occurring in all zoogeographical regions, except Antarctica; the genera *Chamaemyia*, *Neoleucopis* and *Parochthiphila* are also widely distributed, but are notably absent from some regions. Most genera and subgenera, though, are regionally restricted, including several strictly in the Afrotropical Region and several apparently even more restricted. The described Afrotropical fauna is remarkably small, despite the fact that there are numerous undescribed species. Only 12 species in six genera and subgenera are thought to be endemic to the Afrotropics and an additional five species in two other genera and subgenera have been introduced from elsewhere. Two additional genera are recorded here, despite their having no described species in the region, in addition to the recognition of two undescribed genera. Numerous new species are recognised for most genera and subgenera in the region, and all are in need of revision, with no recent identification keys to Afrotropical species available. Although general host information is known for some Afrotropical species, no further information or illustrations are available for the immature stages.

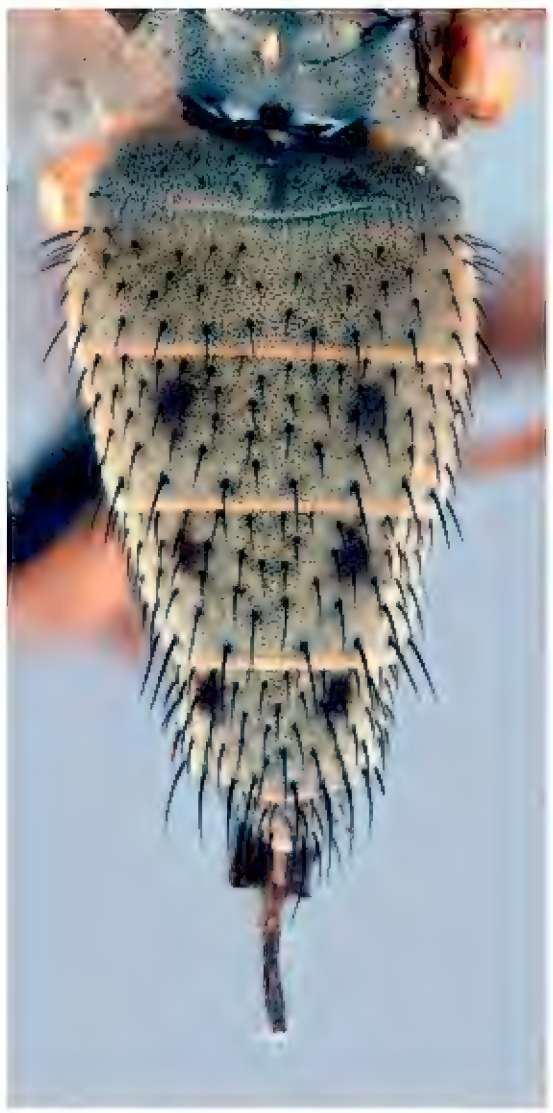
Acrometopia Schiner (Chamaemyiinae: Chamaemyiini)**.** An Old World genus of four described species previously not known to occur in the Afrotropics, except for a vague reference by Cogan (1978: 224), stating that two species in Africa are "… possible derivatives of an *Acrometopia*-like ancestor". None of the Afrotropical species in the genus have been described, although they are easily recognisable and relatively common. The genus can be differentiated from other chamaemyiines by the elongate head, with a receding face, the eye being horizontally elongated (Fig. 29) and the absence of an anepisternal seta (Fig. 2). Although some species of the genus have five dorsocentral setae (1 + 4), few Afrotropical species have been found with this configuration, instead being similar to *Parochthiphila*, with 1 + 3 evenly spaced (as in Fig. 23) or 1 + 2 with a gap where the anteriormost postsutural seta would have been; by way of exception, this gap sometimes contains two greatly reduced setae, suggestive of the 1 + 4 configuration (Figs 2, 3). Specimens of the genus are widely distributed in western Africa, from Kenya through South Africa and in Madagascar and Réunion Is., with numerous undescribed species recognised.

Chamaemyia Meigen (Chamaemyiinae: Chamaemyiini)**.** A widespread genus of 32 described species, occurring in all zoogeographical regions, except the Australasian Region and Antarctica. A single described species, *C. sexnotata* (Thomson, 1869), is recorded from the Afrotropical Region, specifically from South Africa. Specimens of this genus are commonly collected, however, and numerous undescribed species are known from the region, ranging from Ethiopia to Cameroon and south to South Africa and in Madagascar. The genus can be differentiated from other chamaemyiines by the evenly spaced dorsocentral setae in a 1 + 2 configuration (Fig. 5), the anterior fronto-orbital seta being inserted on the frons closer to the lunule than to the posterior fronto-orbital seta (Fig. 31), the lack of an anepisternal seta (Fig. 4) and often having the wing membrane darkened along the costal margin and on crossveins *r–m* and *dm–m* (Fig. 51). This darkening of the wing membrane is common only to the Afrotropical representatives of this genus, apparent in very few species outside the region. All known representatives of the genus are predators as larvae on mealybugs

in the leaf sheaths of grasses and are most frequently collected by sweeping various grasses (Gaimari 2010: 1000).

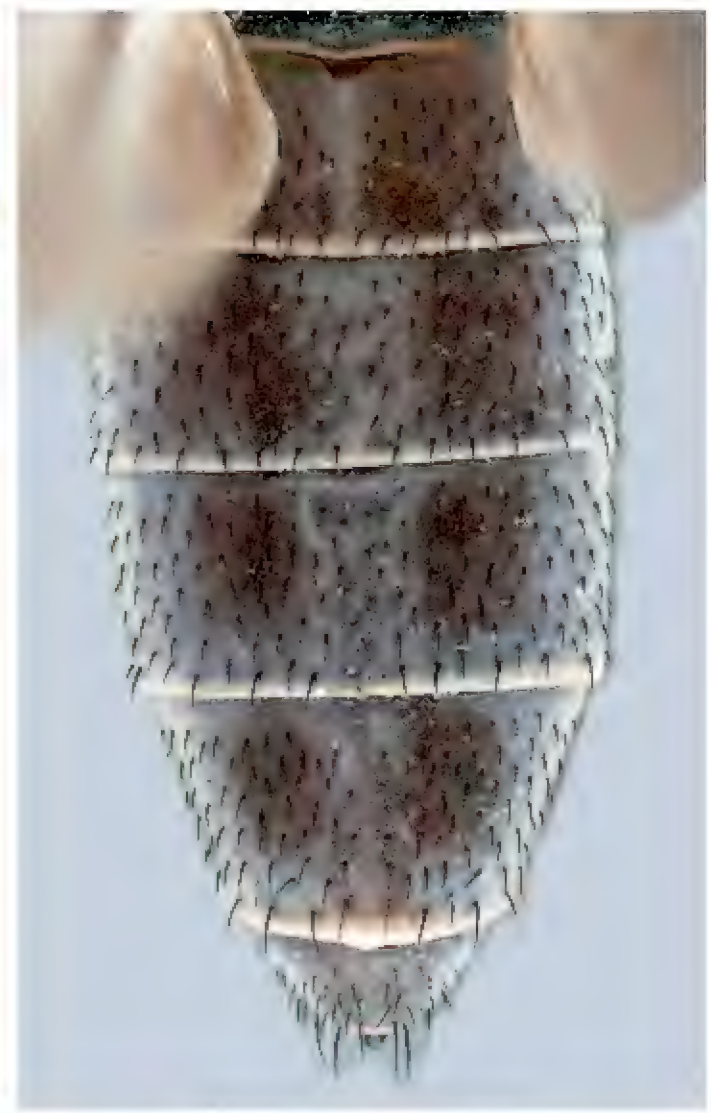
Hamecamyia Gaimari (Chamaemyiinae: Chamaemyiini)**.** An endemic monotypic genus with the single described species, *H. stuckenbergi* Gaimari, 2012, which appears to be endemic to South Africa, as it is only known from a single collecting event in the Drakensberg Mountains, in native scrubby woodlands with streamside grasses. The genus can be differentiated from other chamaemyiines by the absence of a presutural dorsocentral seta (Fig. 7), the absence of a prescutellar acrostichal seta (Fig. 7), the anterior fronto-orbital seta being inserted at about the midpoint between the posterior seta and the lunule (Fig. 33), the lack of an anepisternal seta (Fig. 6) and the darkened wing membrane along the costal cell (c) to the wing tip (Fig. 53). Like other Chamaemyiini, this genus is probably associated with grasses.

Leucopis Meigen (Chamaemyiinae: Leucopini)**.** A genus of 150 described species occurring in all zoogeographical regions



57 *Acrometopia* ♀

58 *Chamaemyia* ♂



59 *Hamecamyia* ♂

60 *Leucopis* (*Leucopis*) ♂

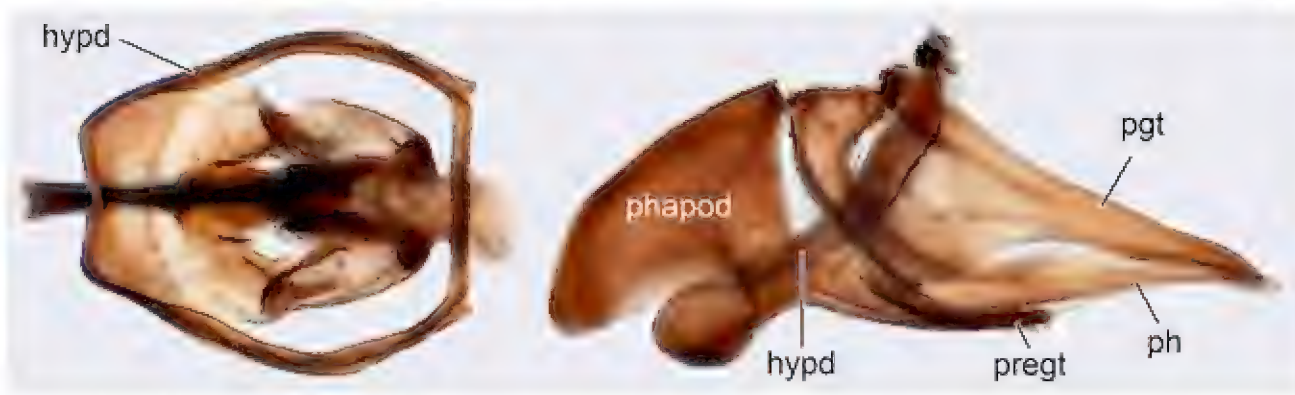
61 *Leucopomyia* ♀

62 *Neoleucopis* ♀

Figs 76.57–62. Abdomens of Chamaemyiidae (dorsal views): (57) *Acrometopia* sp. ♀; (58) *Chamaemyia* sp. ♂; (59) *Hamecamyia stuckenbergi* Gaimari ♂; (60) *Leucopis* (*Leucopis*) sp. ♂; (61) *Leucopomyia* sp. ♀; (62) *Neoleucopis atratula* (Ratzeburg) ♀. Fig. 59 (Gaimari 2012, fig. 8).

63 *Hamecamyia* ♂

64 *Hamecamyia* ♂ 65 *Hamecamyia* ♂

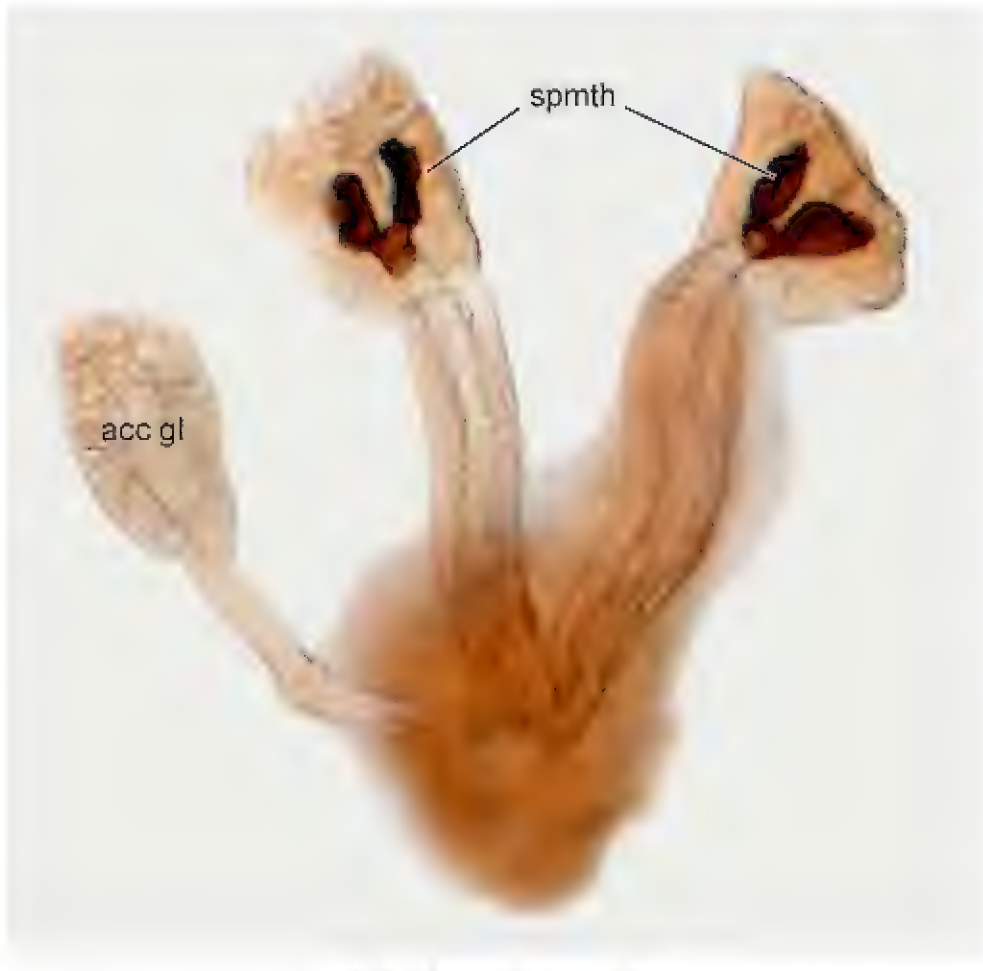


66 *Hamecamyia* ♂ 67 *Hamecamyia* ♂ 68 *Hamecamyia* ♂

Figs 76.63–68. Abdomen and terminalia of Chamaemyiidae: (63) abdomen of *Hamecamyia stuckenbergi* Gaimari, ventral view ♂; (64) same, epandrial complex, lateral view; (65) same, dorsal view; (66) same, hypandrium, dorsal view; (67) same, phallic complex, lateral view; (68) same, phallus, lateral view. Figs 63–68 (Gaimari 2012, figs 11, 13, 12, 15, 17, 18).

Abbreviations: epand – epandrium; hypd – hypandrium; pgt – postgonite; ph – phallus; phapod – phallapodeme; pregt – pregonite; st – sternite; syntgst – syntergosternite; sur – surstylus (fused to epandrium).

except Antarctica, with seven endemic to the Afrotropical Region, in addition to some more widespread species and some introduced for biological control. The genus comprises five subgenera: *L.* (*Indioleucopis* Malloch), *L.* (*Leucopella*), *Leucopis sensu stricto*, *L.* (*Metaleucopis* Tanasijtshuk) and *L.* (*Xenoleucopis* Malloch). Only the subgenera *L.* (*Leucopella*) and *Leucopis sensu stricto* are known to occur in the Afrotropics. The subgenus *Leucopis sensu stricto* is virtually cosmopolitan and is the largest genus-group taxon in the family, with 128 described species, representing more than one-third of all described chamaemyiid species. This subgenus can be differentiated from other leucopines by the typical silvery grey body colour (except for two undescribed black species known from Turkey, with one pruinose and the other shiny), often with goldish to brownish dorsocentral vittae (Figs 1, 11) and paired brown maculae on tergite 3 (Fig. 60), along with absence of prescutellar, anepisternal (Figs 10, 11), ocellar or fronto-orbital setae or setulae (Figs 34, 35) and the acrostichal setulae do not extend posteriorly behind the posterior dorsocentral seta (Fig. 11). The greatest diversity occurs in the northern temperate regions, where the species attack mainly aphidoid Sternorrhyncha (Adelgidae, Aphididae and Phylloxeridae), although some also attack various coccoids (Tanasijtshuk 1986: 201). Despite its great diversity, few species are known from the Afrotropics, although some Palaearctic species, such as *L.* (*Leucopis*) *ninae*, may have been introduced for biological control purposes. The widespread species *L.* (*Leucopis*) *argentata* Heeger, 1848, is also known from Oman, South Africa and Yemen, although the mode of introduction is unknown. The naturally wide-ranging species *L.* (*Leucopis*) *formosana* Hennig, 1938, which occurs throughout Asia and Australia, also occurs in the Afrotropics from Côte d'Ivoire to Yemen and south to South Africa, as well as Cabo Verde and Réunion Is. (Tanasijtshuk 1999). No one particular resource is useful for identifying the described species occurring in the Afrotropics, so Palaearctic literature must be consulted (*e.g.*, Tanasijtshuk 1986: 86), in addition to the fact that there are numerous undescribed species recognised from throughout the Afrotropics. The other subgenus, *L.* (*Leucopella*), was originally described for the species *Leucopis africana* from Kenya, which was recognised as a potentially important predator of the pseudococid *Planococcus citri* on coffee (Kirkpatrick 1926). The subgenus remained monotypic until the species *L. chileana* McAlpine, 1960, was described from South America. The subgenus had only these two species, separated by the oceans, until Gaimari & Raspi (2002) described four new species from north-eastern Africa and an additional species across the Red Sea in Yemen. The subgenus can be differentiated from other leucopines mainly by the presence of one to several setae or setulae along the posterior (or lower) margin of the anepisternum (Figs 8, 9); other characters are diagnostic, but can vary, such as presence of small reclinate ocellar setae (Fig. 9) and, more commonly, prescutellar acrostichal setae (as in Fig. 19). The most widespread species, *L.* (*Leucopella*) *africana*, is known from Eritrea, Ethiopia, Kenya and Tanzania (Chrysantus 2012; Gaimari & Raspi 2002). Two species, *L.* (*Leucopella*) *euryvitta* Gaimari & Raspi, 2002 and *L.* (*Leucopella*) *spatula* Gaimari & Raspi, 2002, are known only from the Eritrean highlands at the north-western edge of the



69 *Hamecamyia*

70 *Ortalidina*

71 *Anchioleucopis*

Figs 76.69–71. Female terminalia and eggs of Chamaemyiidae: (69) spermathecae and accessory gland of *Hamecamyia stuckenbergi* Gaimari, dorsal view; (70) egg of *Ortalidina cellularis* Blanchard, dorsal view (non-Afrotropical); (71) same, *Anchioleucopis geniculata* (Zetterstedt) (non-Afrotropical). Fig. 69 (Gaimari 2012, fig. 23)

Abbreviations: acc gl – accessory gland; spmth – spermathecae.

Great Rift Valley, in the subtropical desert/semi-desert ecozone and *L.* (*Leucopella*) *yaromi* Gaimari & Raspi, 2002, occurs in a similar ecozone in south-eastern Ethiopia. The species *L.* (*Leucopella*) *ardis* is known from the tropical dry forest and savanna ecozone, in the western Great Rift Valley, from Democratic Republic of Congo, Tanzania and Uganda. The species *L.* (*Leucopella*) *gilva* Séguy, 1953, which is here recognised as a representative of this subgenus, is known only from Mauritania and *L.* (*Leucopella*) *vanharteni* Raspi & Gaimari *in* Gaimari & Raspi, 2002, is the only species of the subgenus known from the Arabian Peninsula, in the tropical dry forest and savanna ecozone of Yemen. The described species can be identified using the identification key and descriptions in Gaimari & Raspi (2002), noting that there are several undescribed species in the region. Besides one additional undescribed species known from Ethiopia, there are at least eight undescribed species known from South Africa and one each from Madagascar, Malawi and Namibia. In the Neotropics, there are at least 16 new species of the subgenus known from Argentina and Chile, and two from Ecuador and Peru.

Leucopomyia Malloch (Chamaemyiinae: Leucopini)**.** A genus currently known only from the Holarctic, with four described species occurring in the Palaearctic Region and one in the Nearctic Region. Although no described species are known from the Afrotropical Region, one undescribed species is known from Kenya and Madagascar has at least one additional undescribed species. The genus can be differentiated from other leucopines, firstly by its large size (typically > 3 mm) and by the head height being two (or more) times greater than the length (Fig. 47), the lunule being particularly high (Figs 36, 37), the prescutellar acrostichal setae being usually present (as in Fig. 19), but regardless of that, the acrostichal setulae extend posteriorly to the prescutellum (Fig. 13). Described species are all known to feed exclusively on eggs within female scale insects, mostly in the family Coccidae (Tanasijtshuk 1986: 191), with most feeding on many different soft scale species.

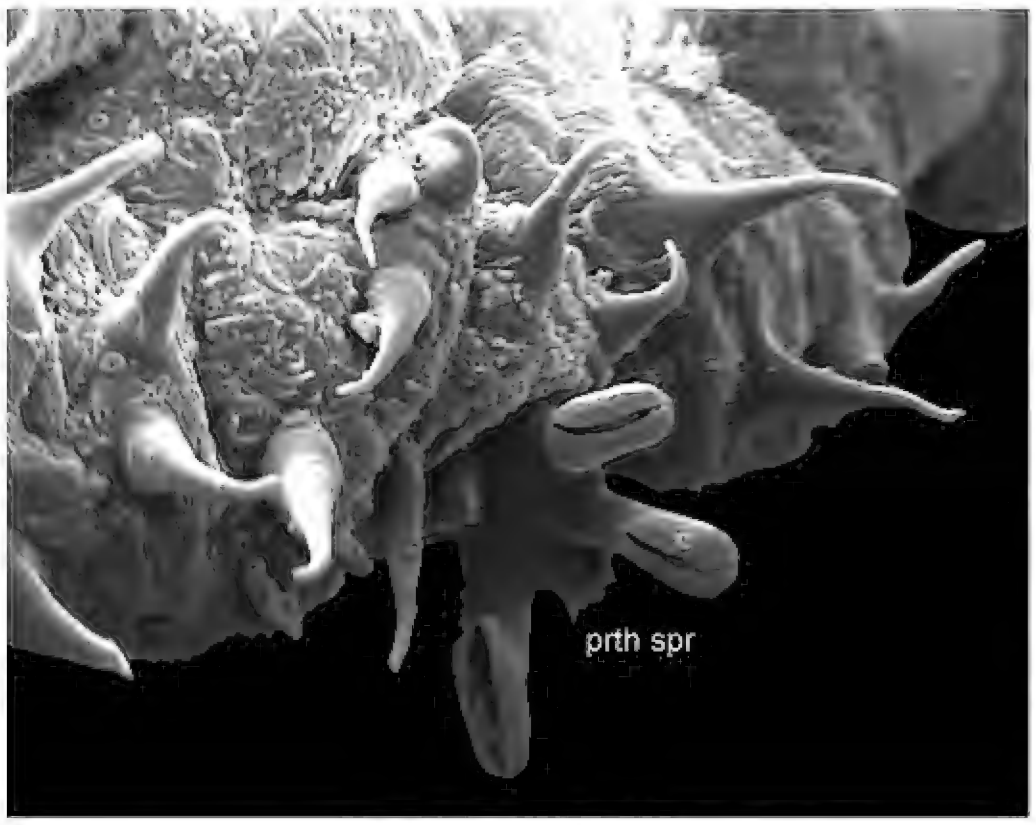
Lipoleucopis de Meijere (Chamaemyiinae: Leucopini)**.** Until recently, a genus known only from one species in the Palaearctic Region. *Lipoleucopis pulchra* Raspi, 2008, was described from United Arab Emirates in the Afrotropics and recorded from Morocco in North Africa (Ebejer 2016). The genus is easily differentiated from other leucopines by its dark grey body colour, the lack of a prescutellum and the costal wing vein (C) ending at vein R_{4+5} (Fig. 56). Besides the two

Figs 76.72–75. Living examples of immature stages of Chamaemyiidae: (72) third-instar larva of *Leucopis* (*Leucopis*) sp. attacking aphids (non-Afrotropical); (73) same, third-instar larvae on leaf; (74) same, puparium, dorsal view; (75) same. Figs 72, 74 (photographs © C. Pilon), Figs 73, 75 (photographs © J. Schneider).

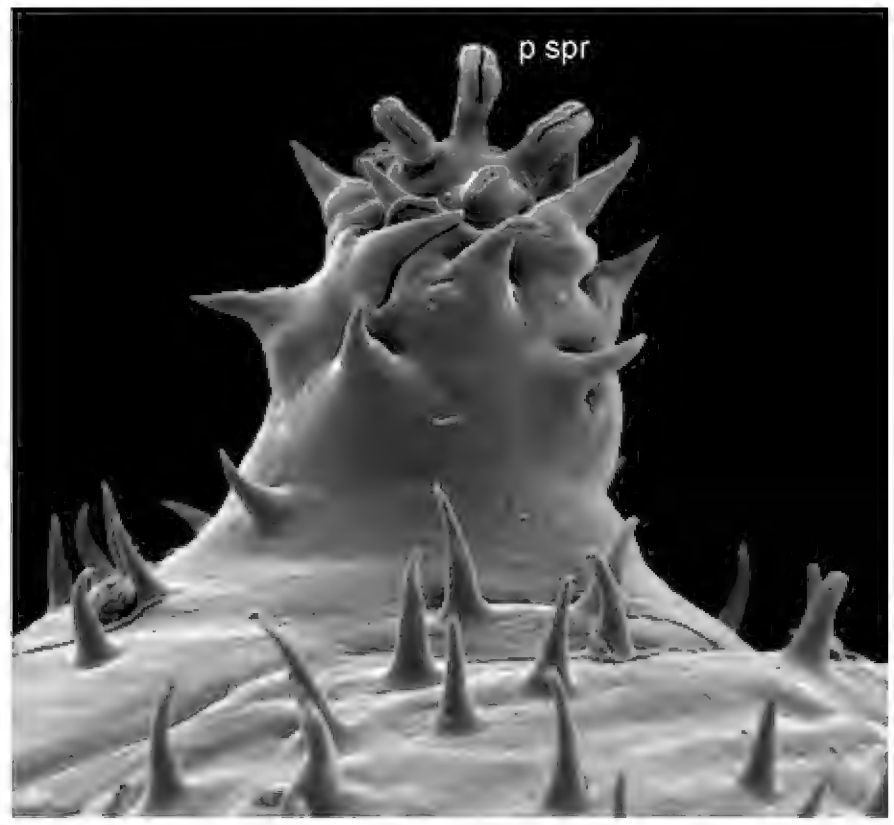
Abbreviations: p spr – posterior spiracle; prth spr – prothoracic spiracle.

described species, no undescribed species are known from the Afrotropics or elsewhere. The biology of the Afrotropical species is unknown, but the Palaearctic species is a known predator of *Pineus pini* on *Pinus sylvestris* (Tanasijtshuk 1986: 158).

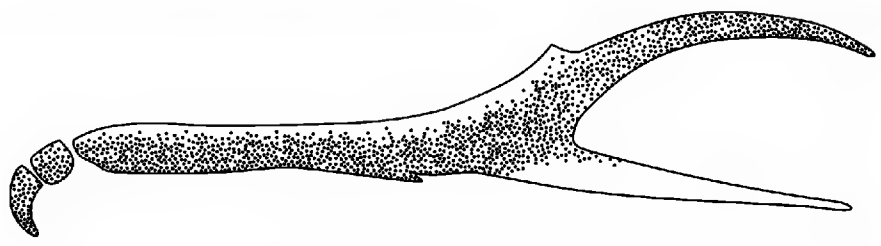
Melanochthiphila Frey (Chamaemyiinae: Chamaemyiini)**.** Only one species of this predominantly Afrotropical genus had been described until recently, *M. nigroaenea* Frey, 1958, confined to Cabo Verde and collected on *Sporobolus robustus* Kunth (Poaceae) on coastal dunes (Frey 1958). An additional undescribed species is recognised from Morocco (Ebejer 2016) and one species was recently described from Saudi Arabia (Ebejer 2017) (both in the Palaearctic). Despite its previously assumed rarity and island endemicity, there are numerous undescribed species sampled across the southern half of the Afrotropical Region, being particularly rich and common in the southern part from Botswana and Namibia, through South Africa. The genus can be differentiated from other chamaemyiines by the black body colour, with at most a light dusting of greyish pruinescence on parts of the thorax and abdomen



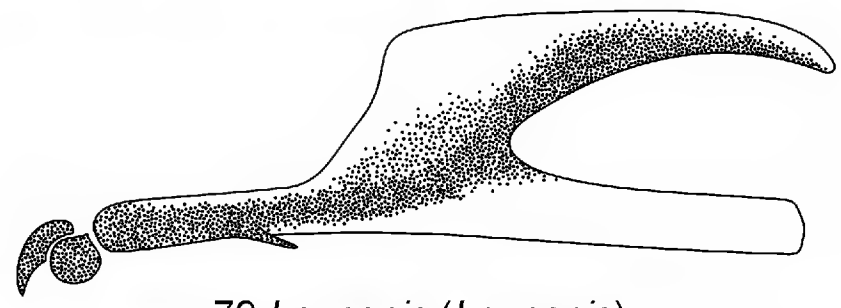
76 *Neoleucopis*



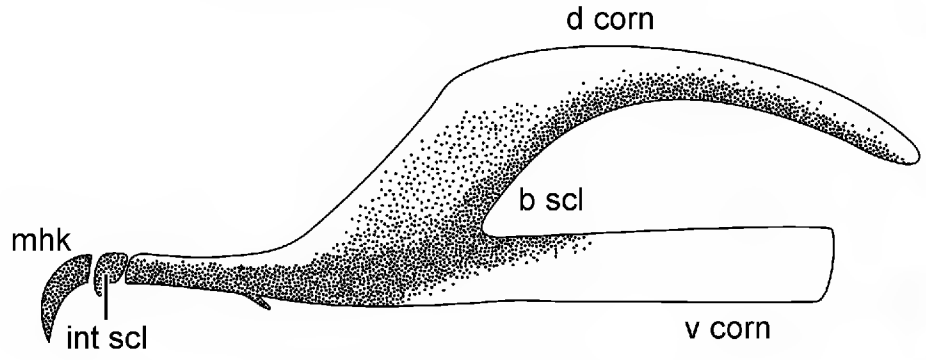
77 *Neoleucopis*



78 *Leucopis* (*Leucopis*)



79 *Leucopis* (*Leucopis*)



80 *Leucopis* (*Leucopis*)

81 *Leucopis* (*Leucopis*)

Figs 76.76–81. Immature stages of Chamaemyiidae: (76) stereoscan micrograph of larval right prothoracic spiracle of *Neoleucopis kartliana* (Tanasijtshuk), lateral view (non-Afrotropical); (77) same, right posterior spiracle, anterodorsal view; (78) cephaloskeleton of first-instar larva of *Leucopis* (*Leucopis*) *ninae* Tanasijtshuk, lateral view (non-Afrotropical); (79) same, second-instar larva; (80) same, third-instar larva; (81) same, inner surface of ventral head region of puparium, dorsal view. Figs 76, 77 (Gaimari *et al*. 2007, figs 7B–C), Figs 78–81 (after Gaimari & Turner 1996*b*, figs 38, 41, 45, 52).

Abbreviations: b scl – basal sclerite; ceph ring – cephalic ring; d corn – dorsal cornu; int scl – intermediate sclerite; mhk – mouthhook; p spr – posterior spiracle; prth spr – prothoracic spiracle; v corn – ventral cornu.

(Figs 14–17), the face and adjacent part of the gena are always glossy black (Fig. 15), the anterior fronto-orbital seta being at least one-third the frons length back from the lunule (Figs 15, 17), the presence of anepisternal seta and dorsocentral setae in the configuration 1 + 3, evenly spaced (Figs 15, 17) (or missing the anteriormost postsutural seta). Species are commonly collected by sweeping grasses, as is common for most Chamaemyiini, but the biology otherwise remains unknown.

Neoleucopis Malloch (Chamaemyiinae: Leucopini)**.** A genus of 14 described species distributed mainly in the Holarctic Realm and Oriental Region, but present through introduction in the Australasian (Tanasijtshuk 1996) and Neotropical Regions. The genus does not occur naturally in the Afrotropics, but several species have been purposefully introduced for biological control efforts, or accidentally introduced with the import of foreign gymnosperm species. As predators of adelgids, they have been of interest for the control of introduced pest adelgid species, such as *Pineus boerneri* in Kenya (Day *et al*. 2003: 106). The genus can be differentiated from other leucopines by the brownish or grey body colour (Figs 18, 19), with a lack of maculae on the abdominal tergites (Fig. 62), the absence of dorsocentral vittae (Fig. 19) and by the presence of small reclinate ocellar setae (Fig. 39). Species of *Neoleucopis* are best separated using the identification key provided by McAlpine (1971), noting that two additional species were later described by Tanasijtshuk (1986: 173) and some clarification of species concepts was provided by Gaimari *et al*. (2007) and Greathead (1995).

Parochthiphila Czerny (Chamaemyiinae: Chamaemyiini)**.** A genus of 28 described species, 27 of which occur in the Palaearctic Region and one is endemic to the Afrotropical Region. Despite the limited distribution of the described species, numerous undescribed species are known from the Nearctic and Neotropical Regions. Two subgenera are recognised, *P*. (*Euestelia*) (Figs 20, 21) with 19 species and *Parochthiphila sensu stricto* (Figs 22, 23) with nine species. Eight of the described species of *Parochthiphila sensu stricto* are known from the Palaearctic (including species in North Africa), with one of them, *P.* (*P.*) *inconstans* (Becker, 1903), also occurring in Oman in the Afrotropical Region (Raspi & Ebejer 2008). There is also a single described species, *P*. (*P.*) *aethiopica* Hennig, 1938, that is strictly Afrotropical, known only from South Africa. All described species of the subgenus *P*. (*Euestelia*) are Palaearctic (including species in North Africa). Both subgenera are diverse and widespread in the Afrotropics, however, with numerous undescribed species. The genus can be differentiated from other chamaemyiines by the head being higher than long or subequal (Figs 20, 22), with the face not receding and the eye elongate vertically (Figs 20, 22), the anterior fronto-orbital seta being inserted at least one-third the frons length back from the lunule (Figs 21, 23), sometimes with a black fascia across the frons between the anterior fronto-orbital setae (Fig. 23), the dorsocentral setae being in a 1 + 3 configuration (Fig. 23), but sometimes with a gap in the place of the anteriormost postsutural seta (Fig. 21). The subgenera can be differentiated by the presence or absence of an anepisternal seta, for *Parochthiphila sensu stricto* (Figs 20, 21) and *P*. (*Euestelia*) (Figs 22, 23), respectively. *Parochthiphila sensu stricto* is widely distributed in eastern Africa, from Ethiopia to South Africa and to Namibia in the south-east and in western Africa from Nigeria to Sierra Leon. The subgenus *P*. (*Euestelia*) is similarly distributed, except it is not known from East Africa, but is known from Madagascar. Like most Chamaemyiini, representatives of this genus are often predators as larvae on mealybugs in the leaf sheaths of grasses and are most frequently collected by sweeping various grasses.

Undescribed genus A (Chamaemyiinae: Leucopini)**.** A genus known only from Kenya, with a single undescribed species. The genus can be differentiated from other leucopines by the dark brown mesonotum (Figs 24, 25) and silvery grey pleuron (Fig. 24), along with a heavily setulose lunule (Figs 40, 41), strong reclinate ocellar setae (Fig. 41), a single strong fronto-orbital seta on the upper half of the frons (Fig. 41) and presence of a prescutellar acrostichal seta (Fig. 25). All known specimens were reared as predators of the coccids *Parasaissetia ficicola* De Lotto and *Saissetia coffeae* (Walker) on *Wurburgia ugandensis* Sprague (Canellaceae) and of a *Ceroplastes* species on *Euclea diviniana* Hiern (Ebenaceae) (S. Gaimari, pers. obs.). In all rearings the larvae were feeding on the scale eggs under the body of the female scale, which is a feeding habit shared with the genus *Leucopomyia*.

Undescribed genus B (Chamaemyiinae: Chamaemyiini)**.** A genus known from two undescribed species, one from Madagascar and one from South Africa. The genus can be differentiated from other chamaemyiines by the absence of a presutural dorsocentral seta (Fig. 27), the presence of a strong prescutellar acrostichal seta (Fig. 27), the position of both fronto-orbital setae being inserted on the posterior half of the frons, with the anterior seta closer to the posterior seta than to the lunule (Figs 42, 43), the absence of an anepisternal seta (Fig. 26) and dense proclinate setulae on the anterior part of the frons (Fig. 43). Being known only from two specimens, very little more can be inferred, although it is possible that it could be associated with grasses, as is the case for most Chamaemyiini.

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COELOPIDAE 77

(Kelp Flies)

Yuchen Ang and Rudolf Meier

Fig. 77.1. Female of *Coelopa alluaudi* Séguy (non-Afrotropical) (photograph © S.A. Marshall).

Diagnosis

[Based on *Coelopa* Meigen; the only genus in the region].

Medium- to large-sized acalyptrate flies (wing length: 5–16 mm), dark brown to black in colour (Figs 1–3), with squat, robust build; often hirsute with mollisetae (large, strongly developed setae basally, but becoming relatively thin and soft apically), especially in larger males; primarily occurring in littoral zones, associated with beached marine algae (mostly Phaeophyceae).

Head (Figs 4, 5) with vertex flat, to slightly convex; occipital region flattened against thorax (Fig. 3); 2–3 fronto-orbital setae present, frontal setae often pointing inwards and intersecting (Fig. 4); antenna decumbent; postpedicel sub-circular; distalmost seta on apical margin of scape enlarged; arista bare (Figs 4, 5); face strongly concave; parafacial process in form of reclinate, angular hook-like structure along epistomal margin (Fig. 3, inset); clypeus large (Fig. 5); gena and occipital region clothed in setae (mollisetae in larger males; Fig. 2); palpus as long as longitudinal length of compound eye (Fig. 6); proboscis large and capitate (Figs 2, 3).

Thorax (Figs 7, 8) broadly flattened and elongate; postpronotum with a few short setulae and 1 large postpronotal seta (Fig. 8); posterior margin of notopleuron extended as sharp, horizontal lamella above wing base; katepisternum with setae in ventral region (mollisetae in larger males) and 1–3 large proclinate setae in posterodorsal region (Fig. 7); katepisternal margin above posterior-most seta projected dorsally as arc into anepimeron; posterior region of katepisternal suture not extended, resulting in insignificant hypopleural channel;

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2021. Manual of Afrotropical Diptera. Volume 3. Brachycera—Cyclorrhapha, excluding Calyptratae. *Suricata* 8. South African National Biodiversity Institute, Pretoria; pp. 1815–1821.

mesonotum with short macrotrichia and distinct row of dorsocentral setae (Fig. 8). Scutellum broad and dorsoventrally compact; with 1–2 pair(s) sub-basal and 1 pair apical scutellar setae, all of similar length (Fig. 8); prosternum enlarged in anterior region, populated with setae (Fig. 9); precoxal bridge absent. Wing (Fig. 10) with membrane hyaline, but sometimes slightly infuscate; costal vein (*C*) unbroken; subcostal vein (*Sc*) complete; vein *CuA+CuP* reaching posterior margin. Legs (Figs 2, 3, 12–15) thick and robust, wholly populated with mollisetae (Figs 2, 3) (males tending to be more hirsute than females); inner side of mid coxa pronounced as rounded, microtrichose mid coxal lobe (Fig. 11); hind tibia with row of ventral curved setae culminating in 2 large subapical anterior setae (Fig. 12); fore basal tarsomere with large scoop-like process (basitarsal thumb *sensu* McAlpine (1991)), on ventral apical margin (Fig. 13); hind tarsomere with similar, but thinner process (Fig. 14); apical tarsomeres depressed and subtriangular; apical margin with 3 setiferous teeth (median tooth less prominent than lateral teeth), tarsal claw simple, scythe-shaped (Fig. 15).

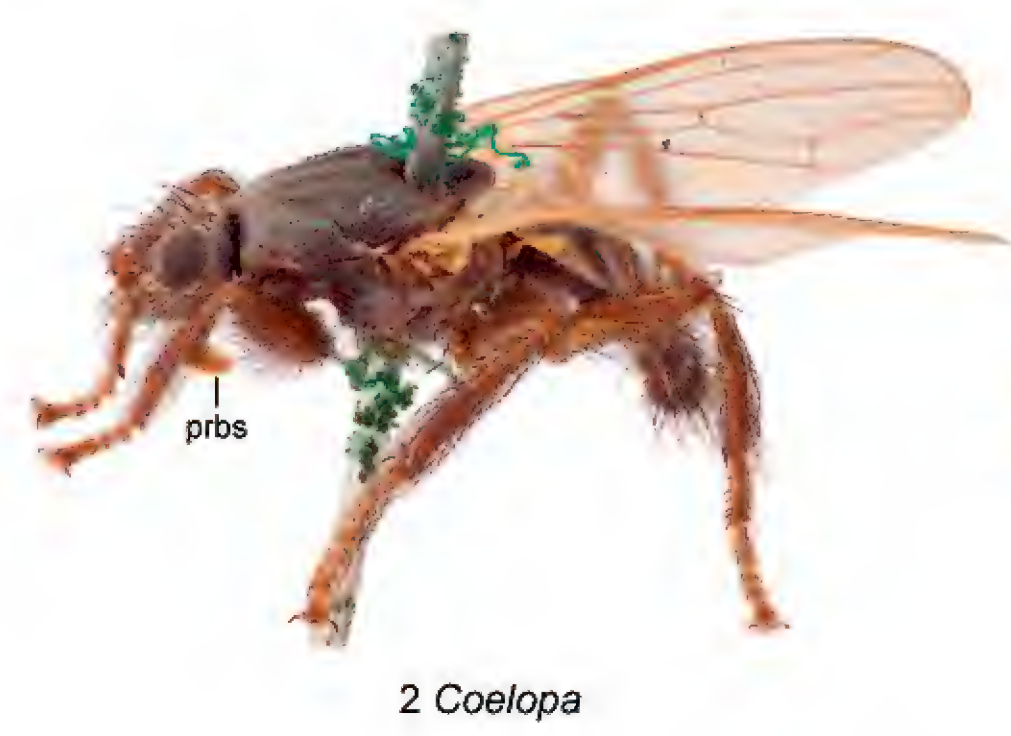
Abdomen with sternite 1 very short and de-sclerotised in antero-medial region; proceeding sternites rectangular and setulose; male tergite 2 onwards populated with mollisetae, especially in larger males (e.g., Fig. 2); abdominal spiracles 1–5 on pleural membrane; tergites and sternites 6 and 7 reduced and de-sclerotised (Figs 16, 17); female tergites setulose (not mollisetae); abdominal spiracles located within tergal sclerites; cercus setulose with 1 large apical seta; internally, with 3 small subspheroid spermathecae (2 as a pair, 1 singly), each with cuticular, pigmented lining (McAlpine 1991); male terminalia (Figs 18–20) with epandrium symmetrical, relatively large and distinct; surstyli in form of long straight processes, setulose on inner margin (Fig. 18); hypandrium rectangular, with pair of slightly projecting, setulose processes in medial region (Figs 19, 20); basiphallus stout, sheathed by 2 pairs of scoop-like lateral sclerites, with membranous bulge on dorsal region; distiphallus flexuous and slender, as long as hypandrial height (Figs 19, 20).

Egg not formally described, the only brief description is that of Phillips *et al.* (1995), where it is mentioned that the sculpture of the upper surface of *Coelopa* eggs have either weak hexagonal sculpturing or a deeply pitted surface, depending on species (*C. frigida* (F., 1805) and *C. pilipes* Haliday, 1838, respectively). Larvae (Figs 21–25) have been described for one Afrotropical species, *C. ursina* (Wiedemann, 1824). Larva of usual schizophoran type, cylindrical; anterior end tapered; posterior end broadly rounded (Fig. 21); pseudocephalon with 2 cephalic lobes; facial mask with numerous combs of cirri becoming progressively larger closer to trilobed lower lip (Fig. 22); maxilla with 4 compound papillae, 3 grouped together medially and one in outer region of maxilla (Fig. 23); respiratory system amphipneustic; prothoracic spiracle on squat, fan-like process, bearing 10–14 glans-like papillae, with terminal spiracular opening (Fig. 24); posterior spiracles separated, on short respiratory tubes; each spiracular disc with 3 circular, slit-like spiracular openings; ecdysial scar adjacent to spiracular disc; peristigmatic tufts furcated, as continuous row around margin of spiracular plate, except around ecdysial scar (Fig. 25). Puparium dark brown, moderately ovoid, with rugose surface.

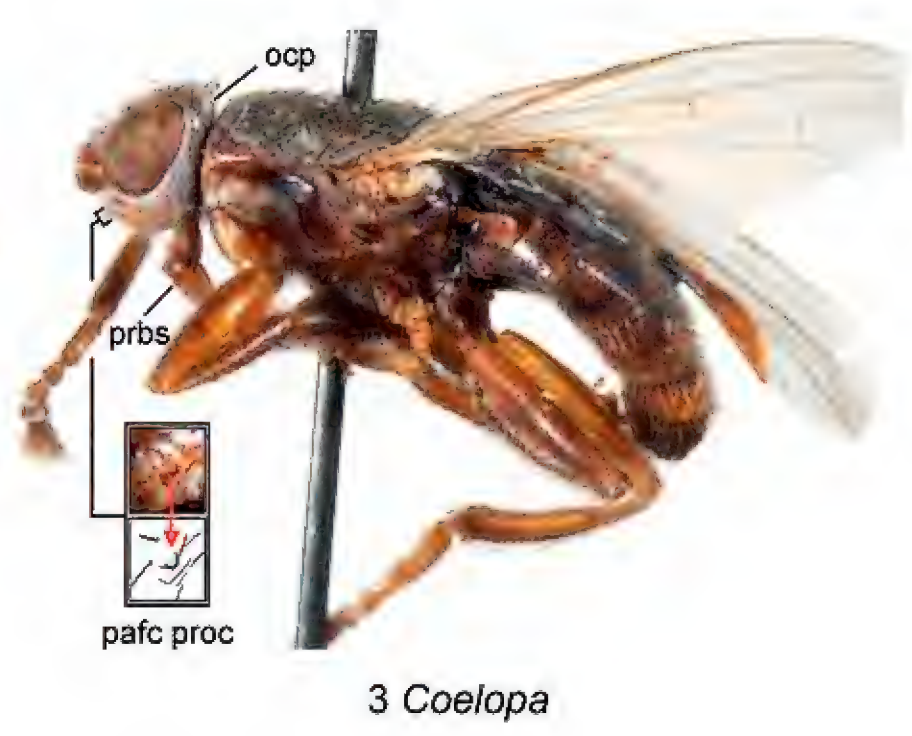
Adult Coelopidae may be superficially confused with non-Afrotropical Helcomyzidae, or certain Anthomyiidae, e.g., *Fucellia* Robineau-Desvoidy (see Chapter 111). They are relatively large and hirsute acalyptrate flies that can be distinguished from other littoral flies based on the following characters: the reclinate and hook-like parafacial process (Fig. 3), setulose metanepisternum (Fig. 7), presence of pubescent mid coxal medial lobe (Fig. 11), presence of setulose teeth on apical tarsomeres (Fig. 15) and large, distinctly shaped male terminalia (Figs 18–20).

Biology and immature stages

All life history stages of coelopids occur in the vicinity of stranded kelp (Phaeophyceae), especially where large wrack beds of kelp and/or other washed-up debris that includes kelp



2 *Coelopa*



3 *Coelopa*

Figs 77.2–3. Habitus of Coelopidae: (2) male holotype of *Coelopa ursina* Wiedemann, lateral view; (3) same, *C. alluaudi* Séguy (inset detail of parafacial process (right side) indicating ventrally directed hook, anterior view).

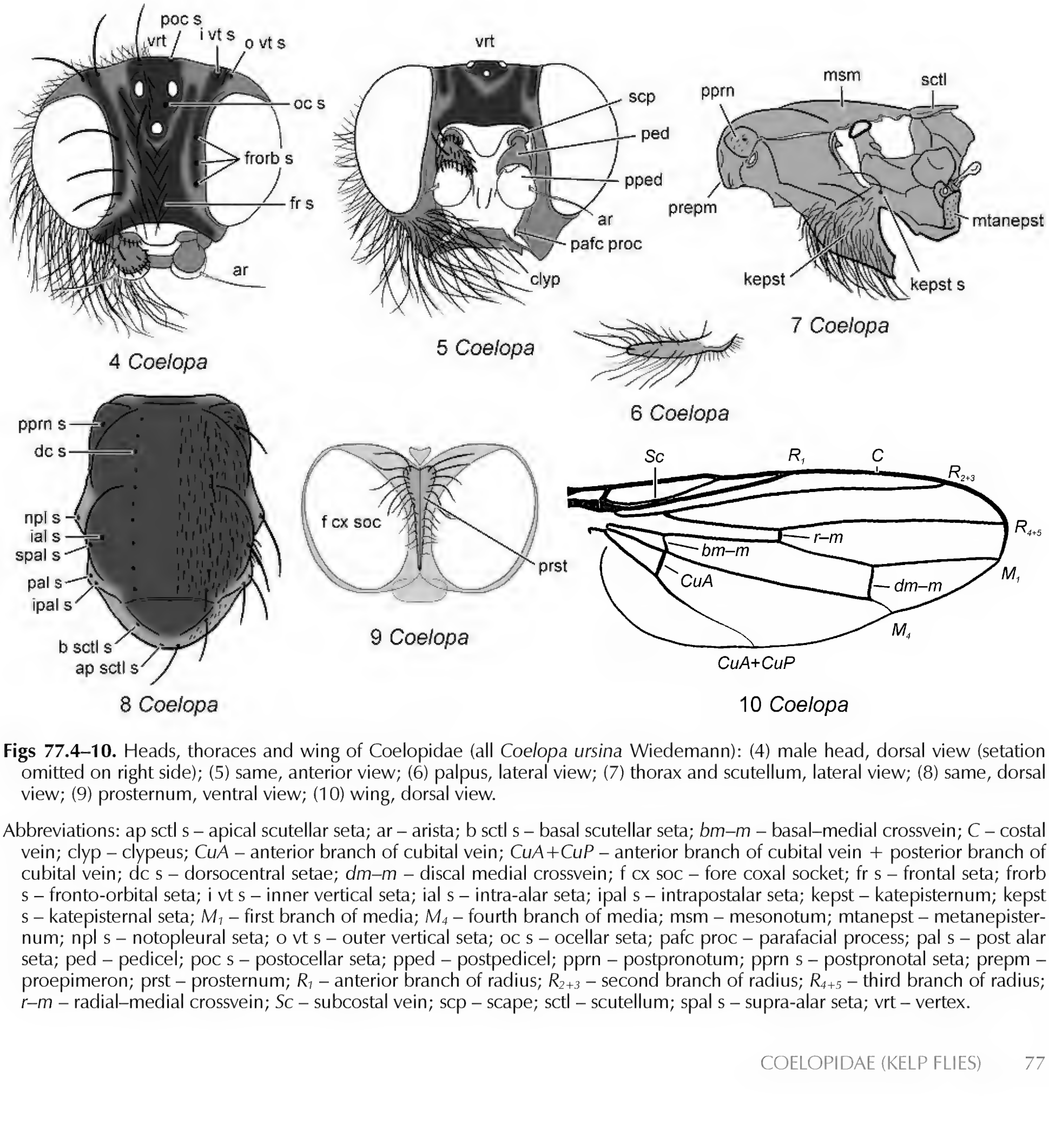
Abbreviations: ocp – occiput; pafc proc – parafacial process; prbs – proboscis.

accumulate (Dobson 1976: 447; Egglishaw 1960; McAlpine 1991). Most coelopid species are temperate, but a few species can also be found in tropical regions (Mathis & McAlpine 2011).

Adults are cursorial and are disinclined to fly. When disturbed, adults fly only short distances in search of the nearest wrack in which to immediately burrow. Life within decaying kelp is the most likely reason for the robust, but streamlined build of the adults, which allows them to burrow easily into kelp and also resist strong winds while clinging to substrates (McAlpine 1991). Puparia are often found in drier substrate (e.g., sand and dry kelp) directly beneath kelp wracks. Coelopids are obligate breeders in decomposing kelp and barring the occasional adult fly sampled inland, are mostly limited to littoral zones.

Many species are morphologically plastic, with large intraspecific variability, especially with regard to body size and hirsuteness. Such differences are partially due to larval nutrition (Hodge & Arthur 1997), but in at least one species (*Coelopa frigida*), it is also linked to a chromosomal inversion, resulting in some individuals being very large, while others are diminutive. These size differences affect mating success rates (Day *et al*. 1996; Gilburn & Day 1994; Gilburn *et al*. 1993).

Coelopid mating behaviour is well-studied for a number of species (e.g., Crean *et al*. 2000; Day *et al*. 1990; Day & Gilburn 1997), including the Afrotropical species *C. ursina* (Crean & Gilburn 1998). Mating typically involves the male mounting the female from behind, with the female shaking



Figs 77.4–10. Heads, thoraces and wing of Coelopidae (all *Coelopa ursina* Wiedemann): (4) male head, dorsal view (setation omitted on right side); (5) same, anterior view; (6) palpus, lateral view; (7) thorax and scutellum, lateral view; (8) same, dorsal view; (9) prosternum, ventral view; (10) wing, dorsal view.

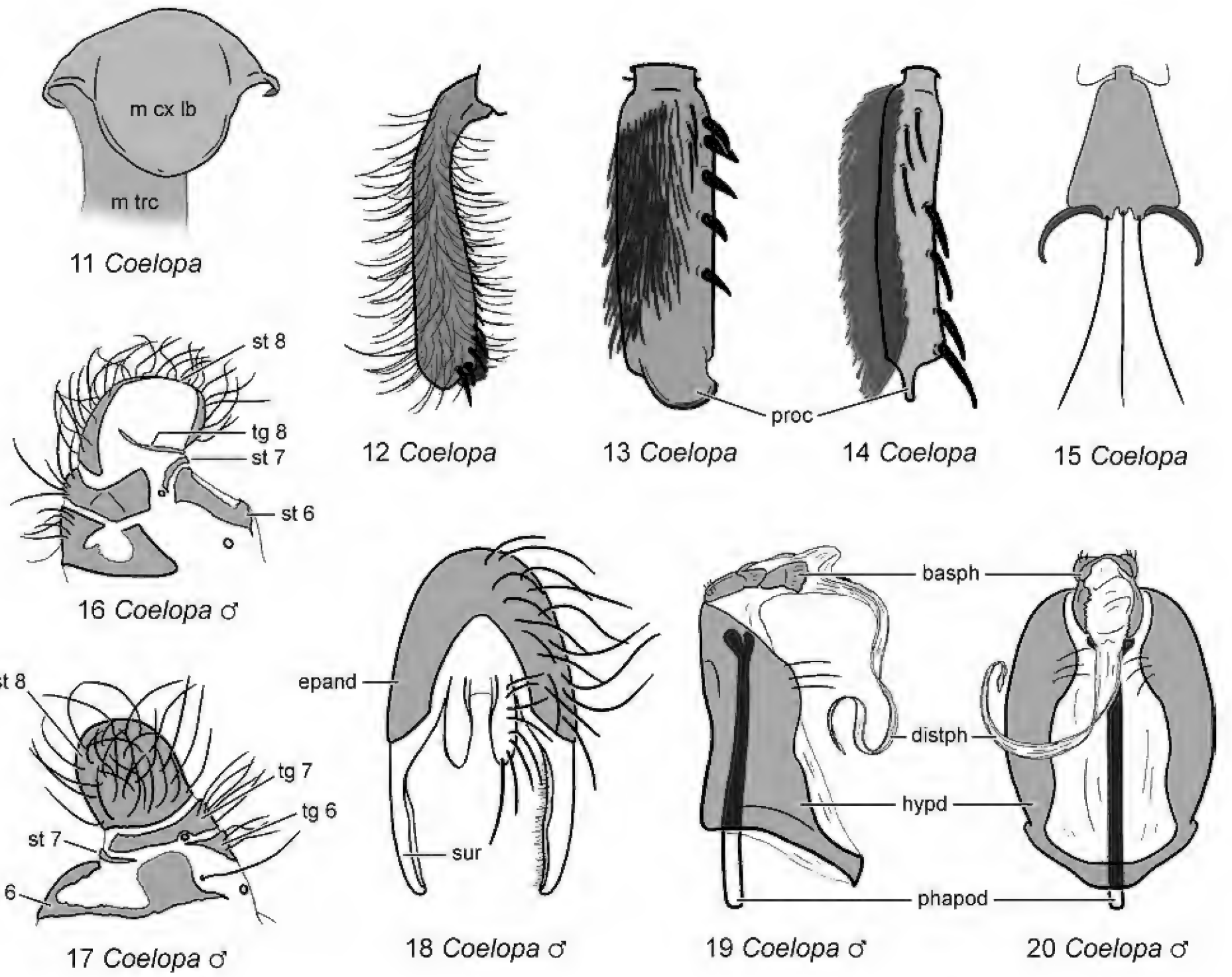
Abbreviations: ap sctl s – apical scutellar seta; ar – arista; b sctl s – basal scutellar seta; *bm–m* – basal–medial crossvein; *C* – costal vein; clyp – clypeus; *CuA* – anterior branch of cubital vein; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; dc s – dorsocentral setae; *dm–m* – discal medial crossvein; f cx soc – fore coxal socket; fr s – frontal seta; frorb s – fronto-orbital seta; i vt s – inner vertical seta; ial s – intra-alar seta; ipal s – intrapostalar seta; kepst – katepisternum; kepst s – katepisternal seta; M_1 – first branch of media; M_4 – fourth branch of media; msm – mesonotum; mtanepst – metanepisternum; npl s – notopleural seta; o vt s – outer vertical seta; oc s – ocellar seta; pafc proc – parafacial process; pal s – post alar seta; ped – pedicel; poc s – postocellar seta; pped – postpedicel; pprn – postpronotum; pprn s – postpronotal seta; prepm – proepimeron; prst – prosternum; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Sc* – subcostal vein; scp – scape; sctl – scutellum; spal s – supra-alar seta; vrt – vertex.

vigorously in an attempt to dislodge the male. This shaking may serve a form of female mate choice (e.g., Day & Gilburn 1997; Day *et al*. 1990). Copulation occurs when a male successfully retains hold of the female. During copulation the male may use the fore basitarsal processes to stimulate the female's antennae (Day *et al*. 1990). In some species males use their mid legs to enclose the female's abdomen, which may be a means for the male to measure female fecundity (Crean *et al*. 2000).

Coelopid larvae feed on the surface of decomposing kelp laminae within wrack beds, where they probably graze on bacterial micro-biota. During high tide, the larvae may burrow into the sand to avoid being washed out to sea. Larvae of some species also ingest air and float when inundated (McAlpine 1991), which may be an adaptation for dispersal *via* marine currents (Dobson 1976: 455).

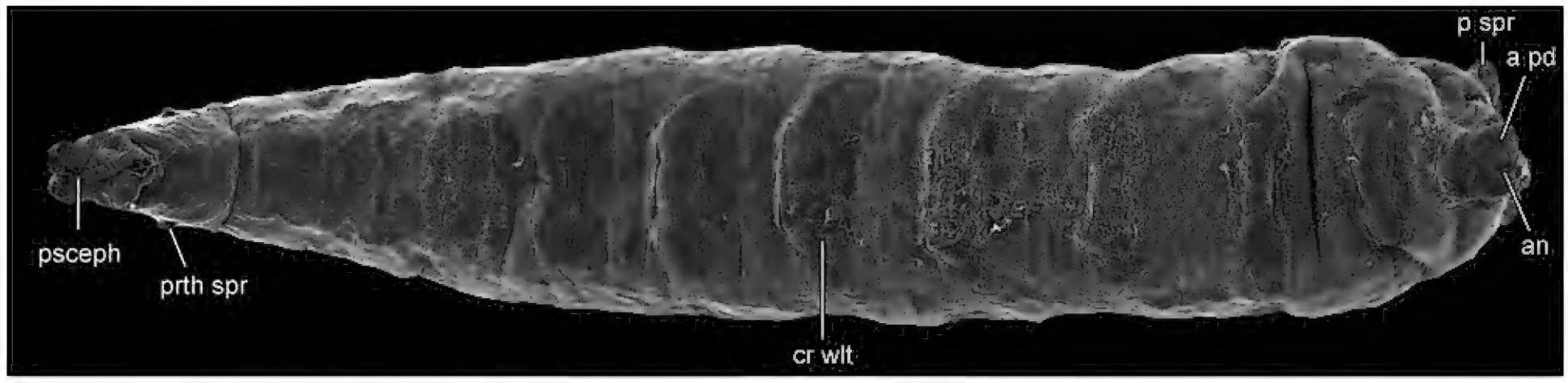
Economic significance

Due to the occasionally high abundance of adults and larvae in kelp beds, coelopids are important decomposers and aid in nutrient recycling (Dobson 1976: 477; Egglishaw 1960; McAlpine 1991). They are also important food sources for other animals, such as birds and reptiles (e.g., Dierschke 1998; Galina *et al*. 1997). Coelopids can form very large swarms and occasionally become nuisances to beach visitors (Oldroyd 1954). Adults are also attracted to certain organic halides and may be attracted to factories that utilise particular solvents

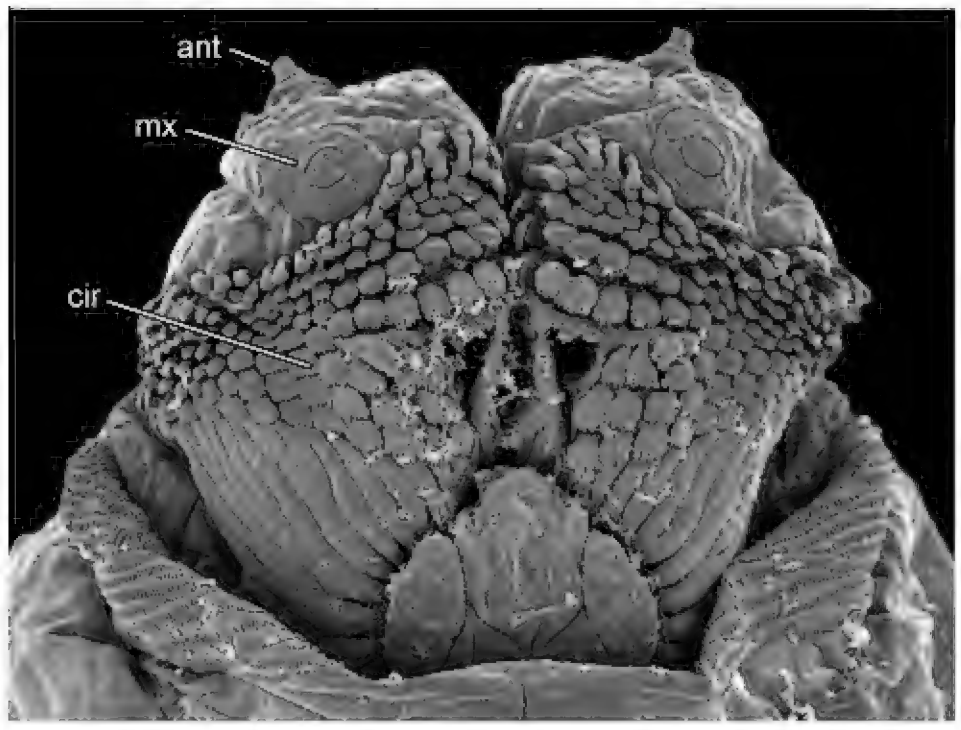


Figs 77.11–20. Legs and terminalia (and associated structures) of Coelopidae (all *Coelopa ursina* Wiedemann): (11) mid coxal lobe, ventrolateral view (left anterior); (12) hind tibia, posterior view; (13) fore tarsomere 1, ventral view; (14) posterior tarsomere 1, ventral view; (15) tarsal claw, dorsal view; (16) male postabdomen, ventral view; (17) same, dorsal view; (18) epandrium, dorsal view; (19) hypandrium and phallus, lateral view; (20) same, ventral view.

Abbreviations: basph – basiphallus; distph – distiphallus; epand – epandrium; hypd – hypandrium; m cx lb – mid coxal lobe; m trc – mid trochanter; phapod – phallapodeme; proc – process; st – sternite; sur – surstylus; tg – tergite.



21 *Coelopa*



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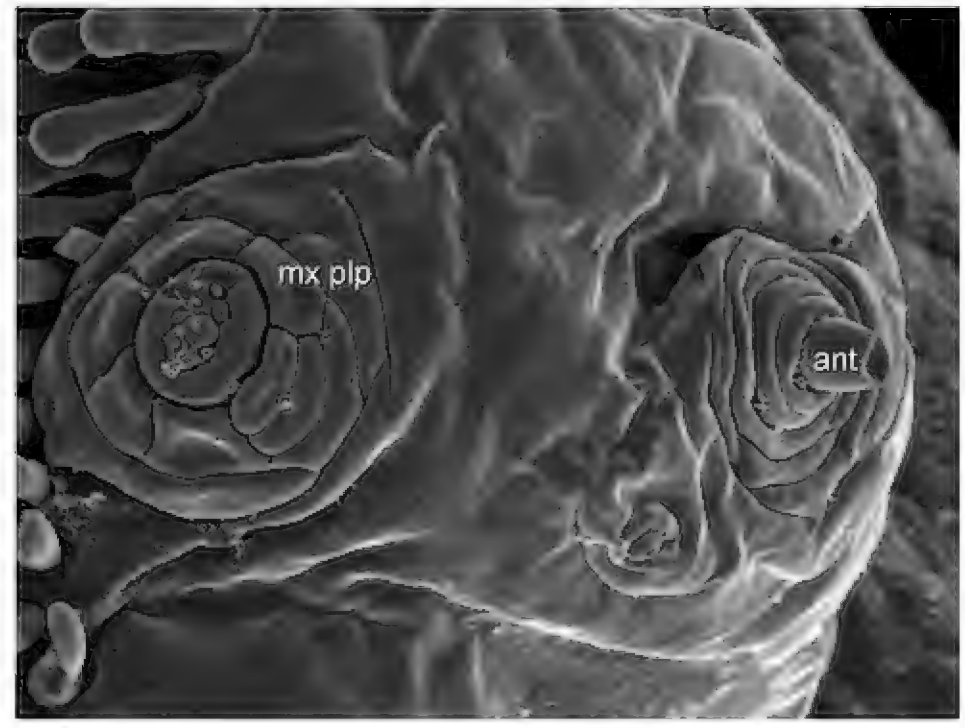
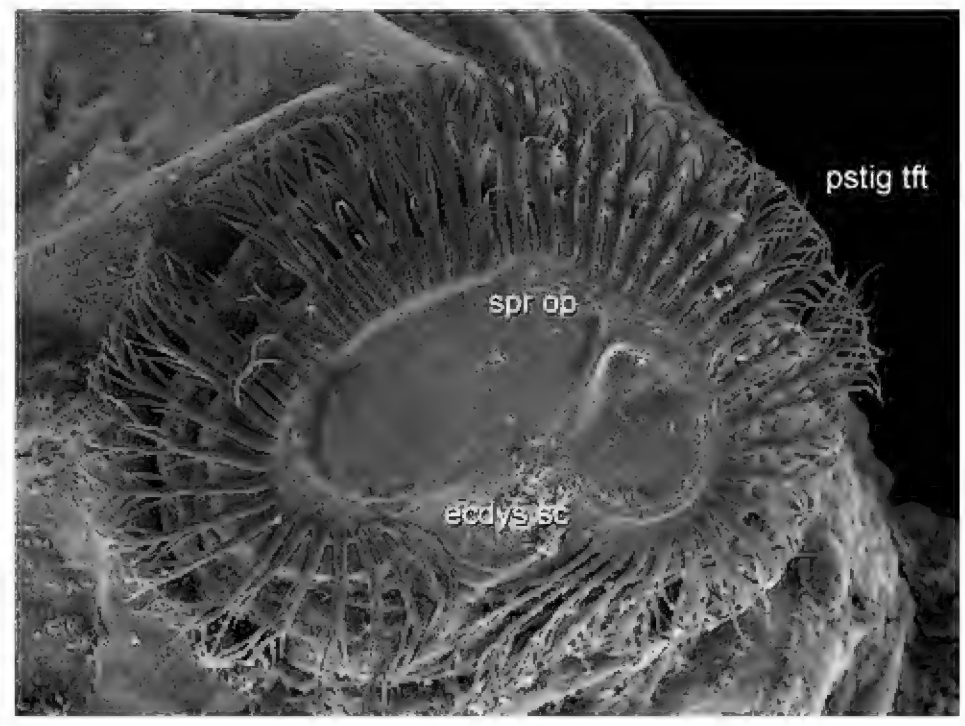


23 *Coelopa*

24 *Coelopa*



25 *Coelopa*

Figs 77.21–25. Scanning electron micrographs of third-instar larva of Coelopidae: (21) habitus of *Coelopa* cf. *alluaudi* (Séguy), ventral view (non-Afrotropical); (22) *C. ursina* Wiedemann, pseudocephalon, ventral view; (23) same, maxilla and antenna, ventral view; (24) same, prothoracic spiracle, lateral view; (25) same, posterior spiracle, caudal view.

Abbreviations: a pd – anal pad; an – anus; ant – antenna; cir – cirri; cr wlt – creeping welt; ecdys sc – ecdysial scar; mx – maxilla; mx plp – maxillary palpus; p spr – posterior spiracle; ppl – papillae; prth spr – prothoracic spiracle; psceph – pseudocephalon; pstig tft – peristigmatic tuft; spr op – spiracular opening.

(Oldroyd 1954; Taylor 1955). Coelopids are not known to be vectors for any human diseases.

Classification

Coelopidae belongs to the acalyptrate grade, while its placement within remains controversial. McAlpine (1991) suggested that the closest relatives are the non-Afrotropical Helcomyzidae, based on shared adult morphological characters, but the most recent analysis of Diptera relationships recovered Coelopidae as sister-group to the non-Afrotropical Helosciomyzidae, albeit with weak support (Wiegmann *et al*. 2011). The monophyly of Coelopidae is supported by morphological data (McAlpine 1991), while a dataset composed of morphological and DNA sequence data yields equivocal results that depend on which analysis method is used (Meier & Wiegmann 2002). Kelp flies were originally described in the family Phycodromidae, based on the genus *Phycodroma* Stenhammar, which was later synonymised with *Malacomyia* Haliday, thus rendering the family name unavailable (refer to Art. 40.2, (International Commission on Zoological Nomenclature 1991). The subsequent proposed family name Coelopidae is based on *Coelopa* Meigen, resulting in an available, but unused Malacomyiidae Czerny. As such, the case to retain the family name Coelopidae should be submitted to the ICZN Commission for decision (McAlpine 1989: 1450; Sabrosky 1999).

Identification

Coelopa is the most widespread and species-rich genus in Coelopidae, with ten species globally. It is also the only genus known from the Afrotropical Region. Previous catalogues of Afrotropical coelopids (Ardö 1964; Cogan 1980: 610; Mathis & McAlpine 2011) list four described species that are currently valid: *C. aequatorialis* Bezzi, 1892, *C. alluaudi* (Séguy, 1941), *C. dasypoda* Bezzi, 1908 and *C. ursina*. According to McAlpine (1991), a fifth named species, *C. africana* (Malloch, 1933), is a junior synonym of *C. ursina*. Diagnostic features for the genus are described above. Some preliminary notes on the status of Afrotropical *Coelopa* are also included in Kirk-Spriggs *et al*. (2001).

Adult specimens are easily collected by swiftly placing wrack into a large, transparent plastic bag and shaking vigorously. The disturbed coelopids will exit the kelp and can be collected from the corner of the bag using vials. Adult coelopids are normally either direct-pinned or micro-pinned in the field for later double-mounting (see Chapter 2).

Synopsis of the fauna

***Coelopa* Meigen.** A genus of ten described species occurring in the littoral zones of all zoogeographical regions, except the Neotropical Region and Antarctica. Five names are available for *Coelopa* species occurring in the Afrotropics (Mathis & McAlpine 2011), with the following distributions: *C. dasypoda*, *C. ursina* and *C. africana* (as a synonym of *C. ursina*) occur on the South African and Namibian coasts; *C. aequatorialis* was described from Somalia; and *C. alluaudi* from Madagascar. The taxonomy of all Afrotropical coelopid species requires revision however. Preliminary observations are as follows: firstly, *C. dasypoda* is likely a synonym of *C. ursina* (Mathis & McAlpine 2011). Bezzi's (1908) description of *C. dasypoda* provides no additional diagnostic differences to Wiedemann's (1824) description of *C. ursina* and the holotype of *C. ursina* (Fig. 2) is identical to Bezzi's (1908) description of *C. dasypoda*. Furthermore, an extensive survey of coelopids from the south-western seaboard of Africa (Kirk-Spriggs *et al*. 2011), including the Skeleton Coast Park of Namibia (type localities for *C. dasypoda* in Bezzi's original description), plus examination of more recent survey material from Namibia's off-shore islands of Ichaboe and Possession, reveal that all specimens belong to a single species that matches the holotype of *C. ursina*. A comparison of the *C. dasypoda* holotype (which was unfortunately unavailable for study) with *C. ursina* may confirm this conclusion, based on the study of recent material. Secondly, the holotype of *C. alluaudi* (Fig. 3) matches Bezzi's (1892) description of *C. aequatorialis* and both occur in the Afrotropical Region (eastern coast). An attempt was made to compare the type material of both species, but the type of *C. aequatorialis* is also unavailable. Finally, *C. alluaudi* is the only Afrotropical species for which the literature indicates that it may also occur in other zoogeographic regions. This is here believed to be erroneous. McAlpine (1991) synonymised Hardy's (1957: 41) *C. palauensis* Hardy, 1957 with *C. alluaudi*. According to him, however, *C. alluaudi* (*i.e.*, *C. palauensis*) lacks a parafacial process, although the holotype clearly possesses such a process (Fig. 3). McAlpine (1991) also provisionally identified specimens from Madagascar (Sainte-Luce near the type locality of Fort Dauphin (= Taolanaro)), as *C. alluaudi*, but did not illustrate the presence or absence of the parafacial process and only described other structures, such as the terminalia (McAlpine 1991: 65). Terminalia may not be a good diagnostic feature to differentiate *Coelopa* species; the terminalia of *C. alluaudi* and *C. ursina* being indistinguishable, for example. Furthermore, examination of all Malagasy coelopid specimens housed in the Zoological Museum, University of Copenhagen, Denmark, revealed that all specimens have a prominent, reclinate hook-like parafacial process. If this feature is constant in *Coelopa* species, it is here suggested that *C. alluaudi* is likely restricted to the Afrotropics.

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SCIOMYZIDAE 78

(Marsh Flies or Snail-killing Flies)

Jean-Claude Vala, Lloyd Knutson† and Raymond M. Miller

Fig. 78. 1. Female of *Sepedon* (*Sepedomyia*) *nasuta* Verbeke (Namibia) (photograph © S.A. Marshall).

Diagnosis

Medium- to moderately large-sized (body length: 2.0–14.0 mm) acalyptrate flies (Fig. 1); compact-bodied or elongate; mainly brown, yellowish brown, blackish, often (many *Sepedon* Latreille species) shiny bluish black, with partly yellowish or reddish legs; wing membrane hyaline or distinctly patterned or mottled; adults usually in aquatic habitats, including permanent freshwater ponds, margins of seasonally inundated areas, forest margins, meadows and clearings, exceptionally dunes and coastal habitats.

Head (Figs 2–7) with antenna porrect (in Tetanocerini), somewhat decumbent (in Sciomyzini); antennal arista sub-basal (except subapical in Palaearctic *Tetanura* Fallén), bare to plumose; ocellar triangle with or without setae (Fig. 2); 1–2 fronto-orbital setae, 1 ocellar seta (0 in *Sepedon* and related genera); 1 postocellar seta, 1 inner vertical seta, 1 outer vertical seta; postocellar and outer vertical setae invariably divergent or parallel (Fig. 2); without vibrissae; ptilinum and ptilinal fissure present (absent in *Sepedon* and related genera).

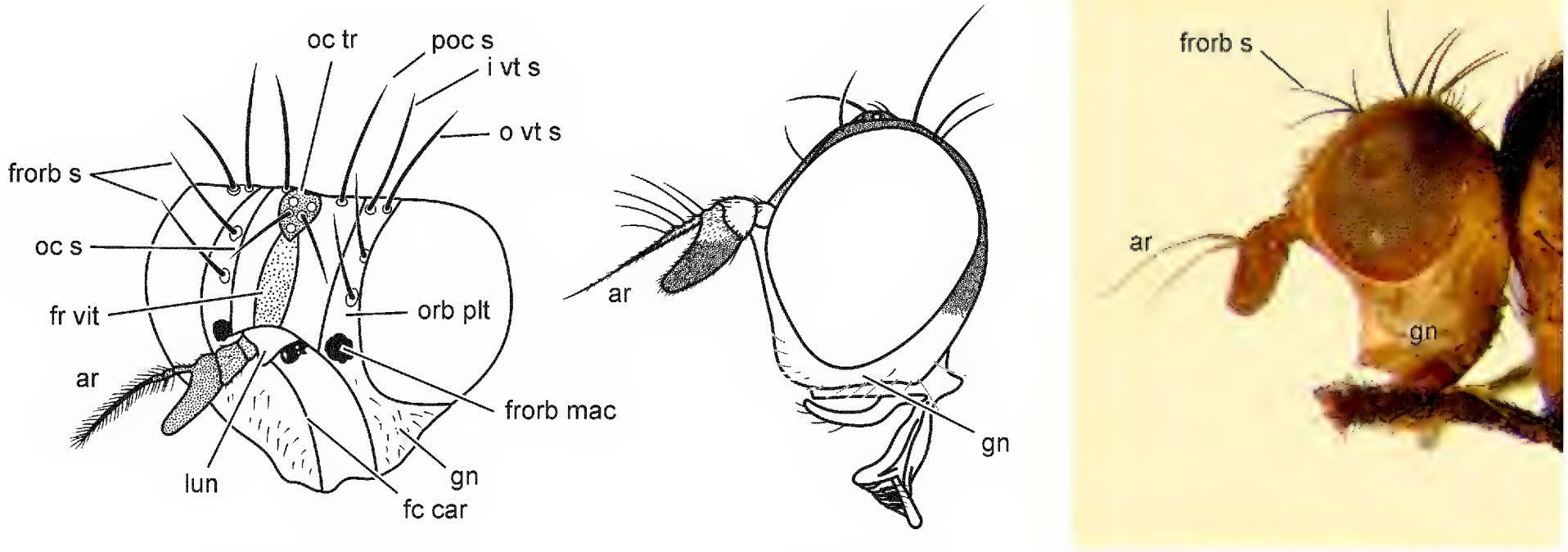
Thorax (Figs 8–11) with lateral chaetotaxy (Fig. 8), with 1 strong proepisternal seta (Sciomyzini), or fine setulae (Tetanocerini); with or without anepisternal setae, if with, then mainly on posterior margin of anepisternum; with or without subalar setae; anepimeron usually with 1 seta; dorsal chaetotaxy (Figs 9–11) complete or reduced (especially *Sepedon*);

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2021. Manual of Afrotropical Diptera. Volume 3. Brachycera—Cyclorrhapha, excluding Calyptratae. *Suricata* 8. South African National Biodiversity Institute, Pretoria; pp. 1823–1846.

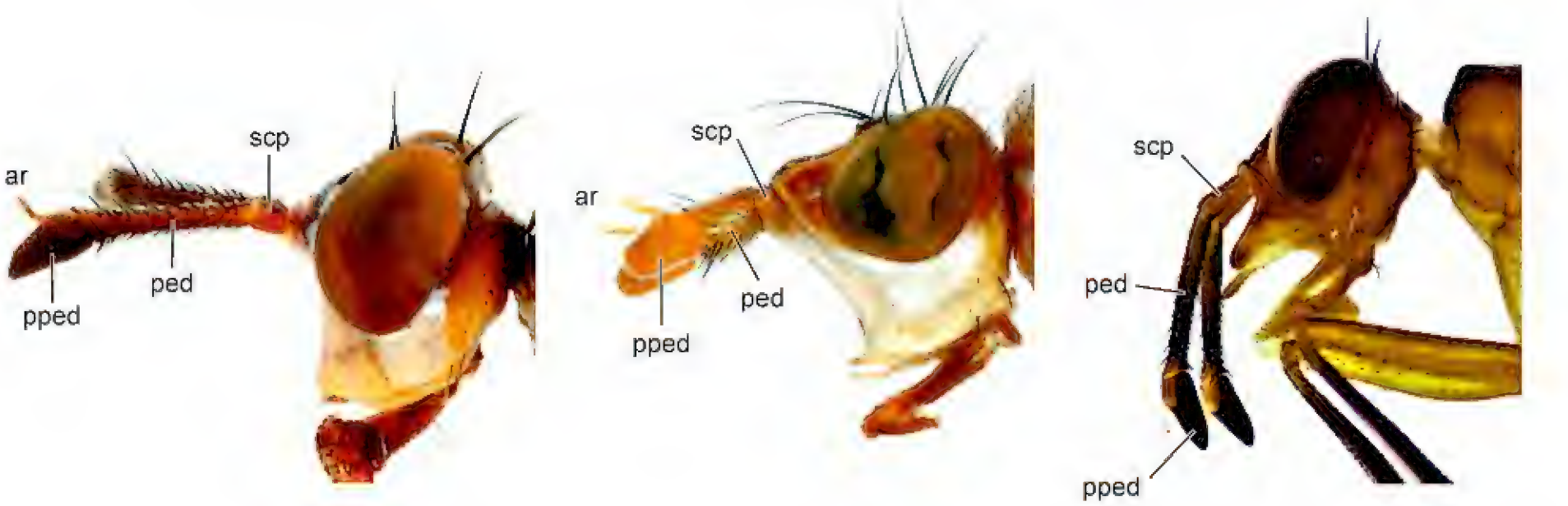
dorsal transverse suture incomplete (Figs 9, 10), complete only in *Sepedoninus* Verbeke (Fig. 11). Wing (Figs 12–26) with muscoid type of venation (e.g., Fig. 12); costal vein (*C*) never broken; subcostal vein (*Sc*) complete; vein R_1 bare (except in some Oriental and Palaearctic Phaeomyiinae); vein *CuA+CuP* reaching margin of wing (except in *Colobaea* Zetterstedt (Fig. 14)). Legs with at least one tibia with preapical dorsal seta.

Abdomen with male postabdominal sclerites (Figs 27, 28) symmetrical to strongly asymmetrical; epandrium (tergum 9) (Figs 27, 28) usually symmetrical, saddle-shaped; both anterior and posterior surstyli present in Sciomyzini (Figs 32–34), in Tetanocerini (Figs 27, 28, 31, 34–36) only posterior generally present, sometimes with vestigial anterior surstylus; male terminalia (Figs 38–42), with or without spiral filaments; unusual sperm pump (= cochleate vesicle, Figs 38, 42) present in some *Sepedon*; female abdomen (Fig. 29), with sternites 6–8 separate or fused into a synsternite; spiracles 1–5 in membrane, 6 and 7 in membrane (Sciomyzini) or in tergites (Tetanocerini); 2 spermathecae present (4 in *Salticella* Robineau-Desvoidy).

Egg (Figs 43–45) elongate, ovoid, apices usually upturned; white immediately following oviposition, becoming slightly greyish; chorion surface with longitudinal grooves, with anastomosing or non-anastomosing ridges and hexagonal reticulation between grooves and ridges; in majority of *Sepedon*



2 Sciomyzidae 3 *Colobaea* 4 *Ditaeniella*



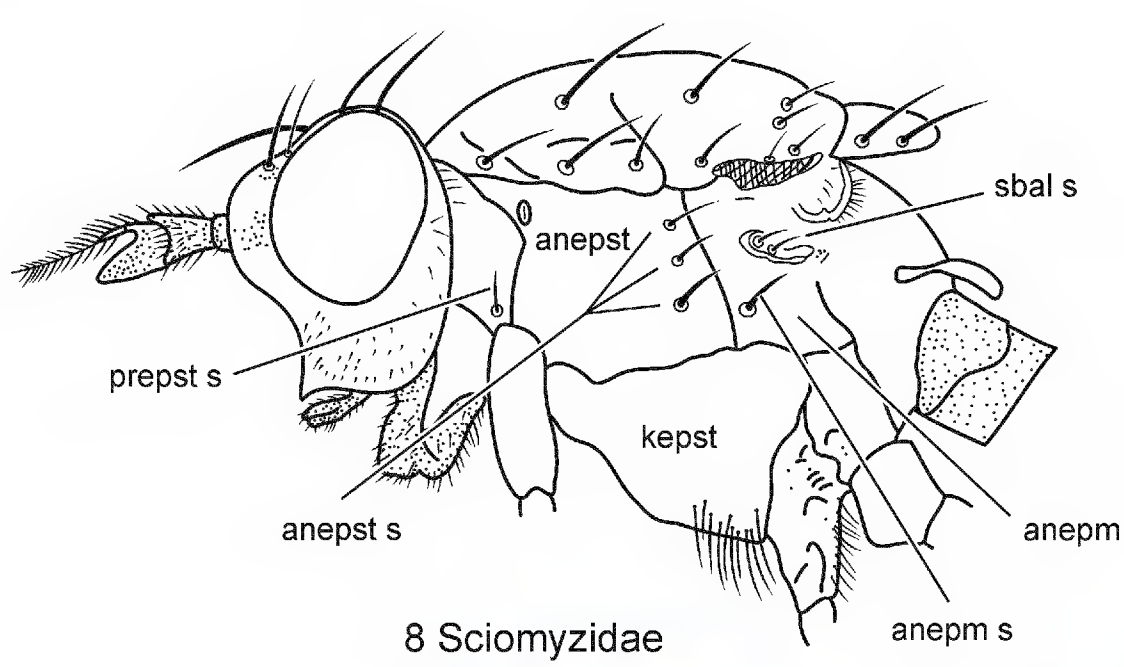
5 *Ethiolimnia* 6 *Sepedon* (*Parasepedon*) 7 *Sepedon* (*Sepedomyia*)

Figs 78.2–7. Heads of Sciomyzidae: (2) schematic diagram of Sciomyzidae head morphology and chaetotaxy, oblique view; (3) head of *Colobaea occidentalis* Knutson & Deeming, lateral view; (4) same, *Ditaeniella* sp.; (5) same, *Ethiolimnia geniculata* (Loew); (6) same, *Sepedon* (*Parasepedon*) *magerae* Verbeke; (7) same, *S.* (*Sepedomyia*) *nasuta* Verbeke, posterolateral view. Figs 2 (after Vala 1989, fig. 2c), Fig. 3 (after Knutson *et al.* 2018, fig. 4); Fig. 4 (courtesy of A.H. Kirk-Spriggs), Figs 5–7 (photographs © S. Hanot).

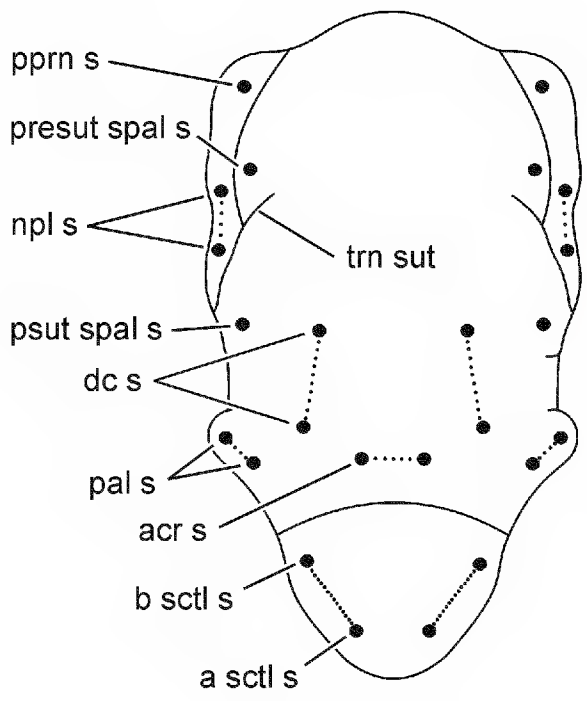
Abbreviations: ar – arista; fc car – facial carina; fr vit – frontal vitta; frorb mac – fronto-orbital macula; frorb s – fronto-orbital setae; gn – gena; i vt s – inner vertical seta; lun – lunule; o vt s – outer vertical seta; oc s – ocellar seta; oc tr – ocellar triangle; orb plt – orbital plate; ped – pedicel; poc s – postocellar seta; pped – postpedicel; scp – scape.

(Fig. 43), 1 well-developed longitudinal dorsolateral and 1 ventrolateral ridge on each side; micropyle on anterior end (Fig. 44), terminal or subterminal, with dorsal lip and aeropyles (Fig. 44); posterior end often knob-like, with (in aquatic species), or without (in terrestrial species), aeropyles (Fig. 45); two eco-morphological types distinguished, according to larval micro-habitat and presence/absence of aeropyles on anterior end only (terrestrial species), or on both ends (aquatic species) (Gasc *et al*. 1984); ventral surface often glued to substrate.

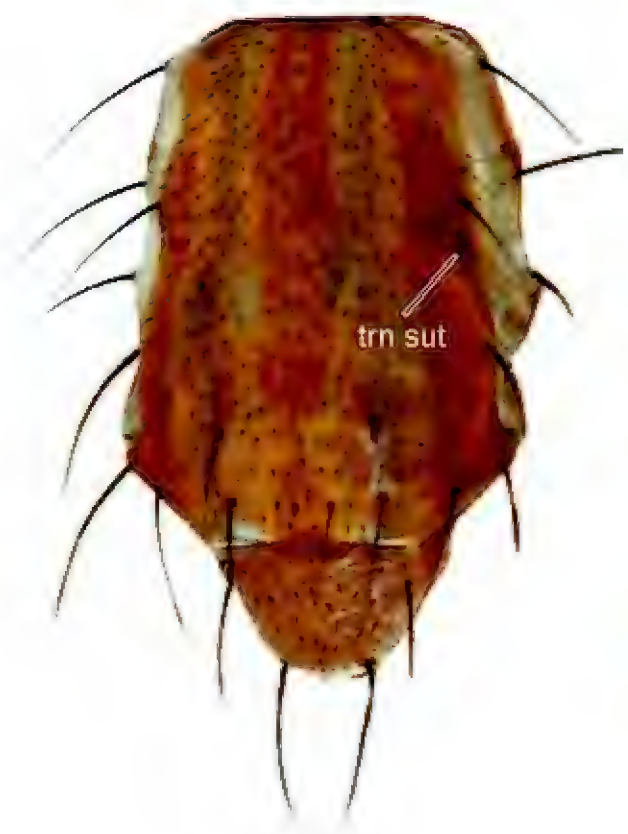
Larva (Figs 46–49) highly variable morphologically, ranging from muscoid type to exhibiting strong adaptations for aquatic existence; body cylindrical, elongate (Fig. 46); anterior end (Figs 46, 47) tapered, posterior end (Fig. 46) usually truncate; integument transparent to slightly pigmented; pseudocephalon anteriorly bilobed (Fig. 47), with anteroventral oral opening (Figs 47, 50); cibarial ridges present only in *Salticella*; 1 pair of maxillary papillae and 1 pair of antennae present (Figs 47, 50); 3 thoracic segments, with 1 pair of extended postpronotal spiracles laterally (Fig. 47), a ventral prothoracic spiculate fold on anterior edge (Figs 47, 50) (= posterior spinule band or patch *sensu* Knutson & Vala 2011: 232), on second- and third-instar larvae only, fleshy base of variable shape, with variable number of spiracular papillae (Fig. 48); each thoracic segment



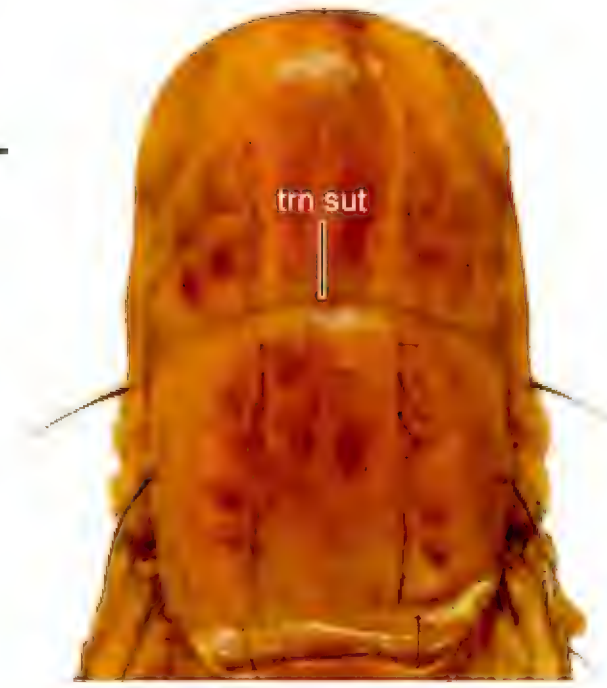
8 Sciomyzidae



9 Sciomyzidae



10 *Ethiolimnia*



11 *Sepedoninus*

Figs 78.8–11. Thoracic features of Sciomyzidae: (8) schematic diagram of Sciomyzidae thoracic morphology and chaetotaxy, lateral view; (9) same, dorsal view; (10) same, *Ethiolimnia geniculata* (Loew); (11) detail of thorax of *Sepedoninus curvisetis* Verbeke, dorsal view. Figs 8, 9 (after Vala 1989, figs 2a, 2b); Figs 10, 11 (photographs © S. Hanot).

Abbreviations: a sctl s – apical scutellar seta; acr s – acrostichal setae; anepm – anepimeron; anepm s – anepimeral seta; anepst – anepisternum; anepst s – anepisternal setae; b sctl s – basal scutellar seta; dc s – dorsocentral setae; kepst – katepisternum; npl s – notopleural seta; pal s – postalar setae; pprn s – postpronotal seta; prepst s – proepisternal seta; presut spal s – presutural supra-alar seta; psut spal s – postsutural supra-alar seta; sbal s – subalar seta; trn sut – transverse suture.

bearing ventrolaterally 1 pair of Keilin's organs (3 sensilla arising collectively from pit, Fig. 51); 8 abdominal segments, with or without weak, transverse intra-segmental grooves; ventral and lateral tubercles bearing sensilla (Tetanocerini), or variable rows of creeping welts on some segments ventrally (Sciomyzini); last segment truncate, with 2–5 pairs of developed peripheral fleshy lobes (Fig. 49); posterior spiracles with 3 developed peristigmatic tufts inserted between 2 or 3 spiracular openings on each spiracular plate (Figs 49, 52); cephaloskeleton (Figs 53–59) genus specific; dental sclerite (= ventral arched sclerite *sensu* Knutson & Vala 2011: 231) with anterior edge denticulate (Fig. 56) (characteristic for family), joined to anteroventral margin of paired mouthhooks; labial sclerite (= ligulate sclerite *sensu* Knutson & Vala 2011: 231) (Figs 53, 57) inserted between anterior arms of intermediate sclerite; posterior part of intermediate sclerite sometimes fused to anterior base of parastomal bars; dorsal bridge present between dorsal cornu of paired basal sclerites in *Salticella* and Sciomyzini; accessory teeth on mouthhook in Tetanocerini (Figs 53, 55, 58, 59).

Puparium (Figs 60–69) mostly ovoid, barrel-shaped (except strongly modified if pupariation occurs within snail shells or in water); integument opaque, white or yellowish (immediately following pupariation), becoming light or dark brown, with vestiges of third-instar larva.

Adult Sciomyzidae (Fig. 1) can be distinguished from other Acalyptratae by the characters outlined by Knutson & Vala (2011: 271). The clypeus is not exposed as in Ephydridae (see Chapter 100) and several other Acalyptratae; the ptilinal fissure is present at least dorsally (except in some *Sepedon*), with a distinct lunule as in other Schizophora, thus excluding Lonchopteridae (see Chapter 58), Platypezidae (see Chapter 57) and Phoridae (see Chapter 59); the antenna comprises a scape, pedicel and postpedicel and a sub-basal arista, inserted directly on the dorsum and not on a frontal prominence as in Conopidae (see Chapter 66); the pedicel lacks a longitudinal, dorsal seam as in Calyptratae and some other Cyclorrhapha; the vibrissae are absent, thus excluding some Calyptratae, such as Anthomyiidae (see Chapter 111) and Scathophagidae (see Chapter 110); and the calypteres are small and do not extend beyond the halteres, as they do in most Calyptratae.

Biology and immature stages

Adults do not fly for long distances and occur mostly near or on low biotope vegetation occupied by their potential hosts/prey, which include various freshwater or terrestrial Mollusca (including slugs), freshwater Oligochaeta, or even millipedes (Diplopoda) (see below). Generally, adults settle on vegetation with the head directed downwards (e.g., Fig. 1).

Depending on the species, females (e.g., numerous *Sepedon* species) oviposit individual eggs, or aligned egg masses, glued by their lateral surfaces to emergent vegetation. Some sciomyzids oviposit on various specific substrates (e.g., soil, moss, grasses, *etc.*), frequented by their hosts/prey, and in such cases, some larvae fail to locate prey and perish. In some species, however, females oviposit directly onto the host/prey to be consumed by the larvae, and in such cases, larval losses are far less and the rate of larval maturation considerably higher. According to Vala *et al.* (1995), the Afrotropical sciomyzid *Sepedon* (*Parasepedon*) *trichrooscelis* Speiser, 1910, oviposits directly on the shells of semi-aquatic (or hygrophilous) Afrotropical molluscs of the genus *Succinea* Draparnaud (Succineidae). During larval development, feeding behaviour changes from parasitoid to saprophagous types, as confirmed by Knutson (2008), based on laboratory rearings with the Nearctic mollusc *Succinea campestris* Say.

Following hatching, first-instar larvae move directly to a water body in search of their hosts/prey. Larvae are mainly aquatic predators. Each can partially, or entirely, consume up to 20–30 molluscs during development. The number of prey items killed or consumed, increases as the larva develops in relation to the size proportion of prey/larva.

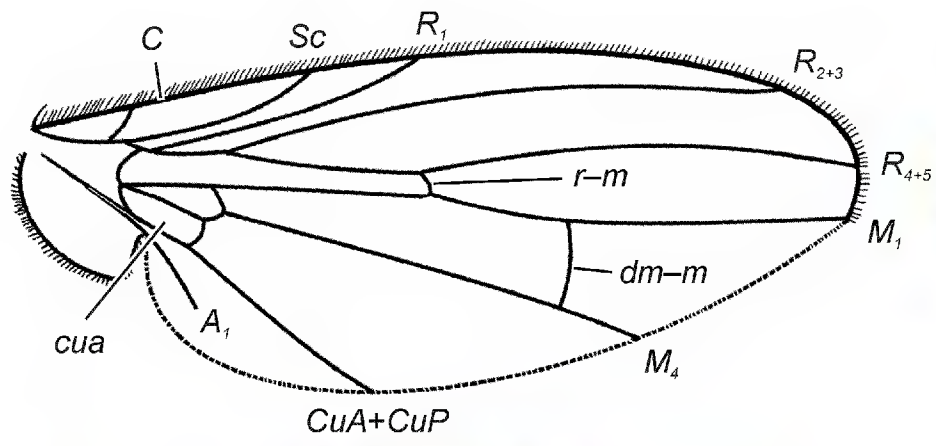
To date, the life histories and biologies of 240 of the known 543 Sciomyzidae species, in 41 of the 61 genera, have been described. These include predominantly extralimital species in the Nearctic and Palaearctic Regions (numbers of species are often modified according to additions and synonymies). Knutson & Vala (2011) provided a detailed overview of the family, which contains much additional information on life histories and biologies.

Larvae of most species predate on non-operculate (pulmonate) freshwater gastropods (Figs 70, 71). A few attack coastal/marine Littorinidae or operculate freshwater gastropods, such as *Valvata* O.F. Müller species; eggs and/or juveniles of Lymnaeidae, Physidae or Succineidae; and a few attack Sphaeriidae (Bivalvia). Larvae of many species attack various non-operculate terrestrial gastropods, including slugs and hygrophilous/semi-aquatic Succineidae. During their development, many larvae combine diverse feeding behaviours, ranging from strict predators, predators/saprophages and predators/parasitoids to strict parasitoids. Thus, feeding on gastropods has been considered as one of the distinctive characters of the Sciomyzidae. A few non-malacophagous behaviours have been reported recently however. Remarkably, two Afrotropical species consume only freshwater oligochaetes (Vala & Gbedjissi 2011; Vala *et al.* 2000*a*, 2002) (Fig. 72). The sole biologically studied species of Phaeomyiinae, the Palaearctic *Pelidnoptera nigripennis* (F. 1794), is an internal parasitoid of only millipedes (Diplopoda: Julidae) (Bailey 1989; Baker 1985; Vala *et al.* 1990, for the complete life cycle). In general, biological studies include ecological aspects, larval feeding behaviour and hosts/prey interactions, morphology of immature stages, phenological differences, and more recently, genetic and phylogenetic aspects. Based on morphology and length of the peripheral lobes on the caudal abdominal segment and the shape and size of the peristigmatic tufts, Vala & Gasc (1990) delimited four eco-adaptations of larvae, *i.e.*, truly aquatic, semi-aquatic, semi-terrestrial and truly terrestrial.

Berg (1964: 278) and Berg *et al.* (1959) speculated on some possible aspects of the evolution of predator/prey relationships in snail-killing sciomyzid larvae. Following on from subsequent extensive biological studies, Knutson & Vala (2002) proposed 15 behavioural groups, based on the kind of hosts/prey feeding behaviour and larval habitats/micro-habitats. They mapped (1) behavioural groups; (2) major categories of hosts/prey of sciomyzid genera; and (3) characters of the immature stages of genera onto the cladogram of Marinoni & Mathis (2000; based on adult characters) to provide an evolutionary scenario.

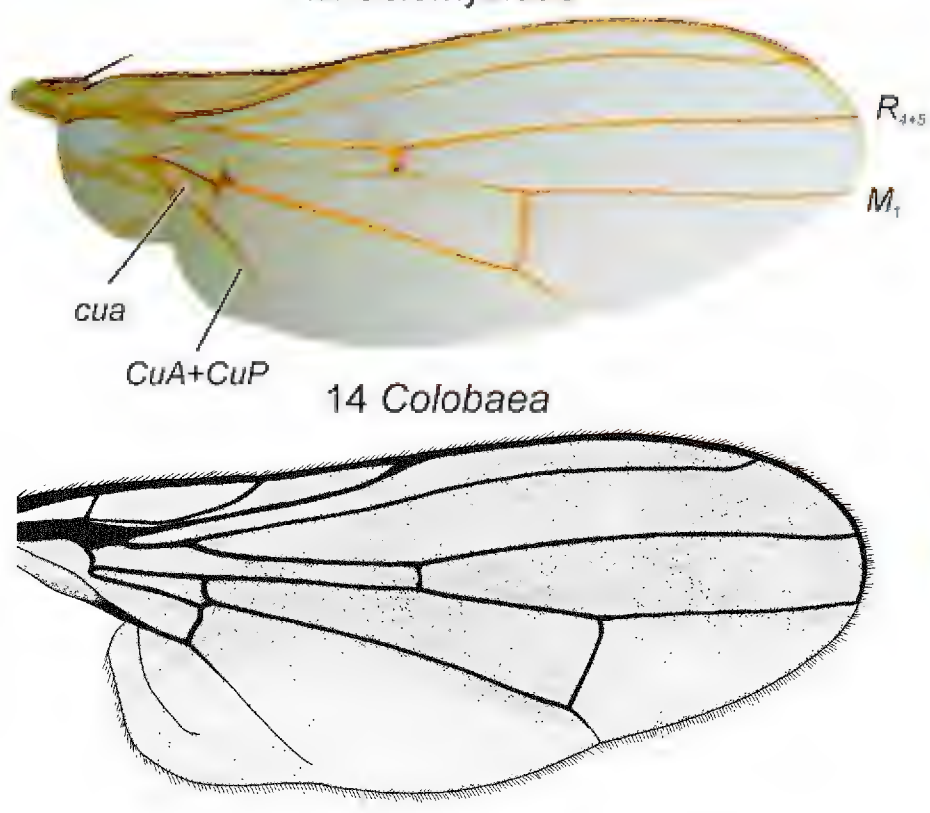
Placement of Phaeomyiidae as a subfamily of Sciomyzidae by Tóthová *et al*. (2012), a group of millipede-feeders, based on larvae of *P. nigripennis*, was included by Vala *et al*. (2012). The Afrotropical species, of which the life histories of 13 species in four genera are published or are in preparation, can be classified in the following behavioural group number established by Knutson & Vala, 2002; Behavioural group 1, facultative, opportunistic predators/parasitoids/saprophages, that feed on dead, moribund, or living snails, *Salticella stuckenbergi* Verbeke, 1962 (Miller 1995); Behavioural group 2, predators/saprophages of non-operculate (pulmonate), primarily freshwater snails, exposed on moist surfaces by receding or fluctuating water levels, or while they are foraging or migrating, *Ditaeniella grisescens* (Meigen, 1830); Behavioural group 4, parasitoids or parasitoids/predators of hygrophilous, semi-terrestrial Succineidae snails, *Sepedon* (*P.*) *hispanica* Loew, 1862 and *S.* (*P.*) *trichrooscelis*; Behavioural group 7, predators/saprophages of non-operculate terrestrial snails, *S.* (*P.*) *ornatifrons* Adams, 1905 and *S.* (*P.*) *umbrosa* Verbeke, 1950; Behavioural group 11, predators of non-operculate snails at or just below the water surface, just above the surface on emergent vegetation, and occasionally, on snails exposed on moist, "shoreline" surfaces, *S.* (*S.*) *aenescens* Wiedemann, 1830, *S.* (*P.*) *neavei* Steyskal, 1956, *S.* (*P.*) *ruficeps* Becker, 1923, *S.* (*P.*) *scapularis* Adams, 1903, *S.* (*P.*) *testacea* Loew, 1862 and *Sepedoninus curvisetis* Verbeke, 1950; and Behavioural group 15, predators of freshwater oligochaete worms, *Sepedon* (*Mesosepedon*) *knutsoni* Vala, Gbedjissi & Dossou, 1994 and *Sepedonella nana* Verbeke, 1950, also alternative prey of the primarily malacophagous *Sepedon* (*P.*) *ruficeps*.

In an analysis of the potential of Sciomyzidae as biological control agents, mainly against terrestrial gastropods, Barker *et al*.

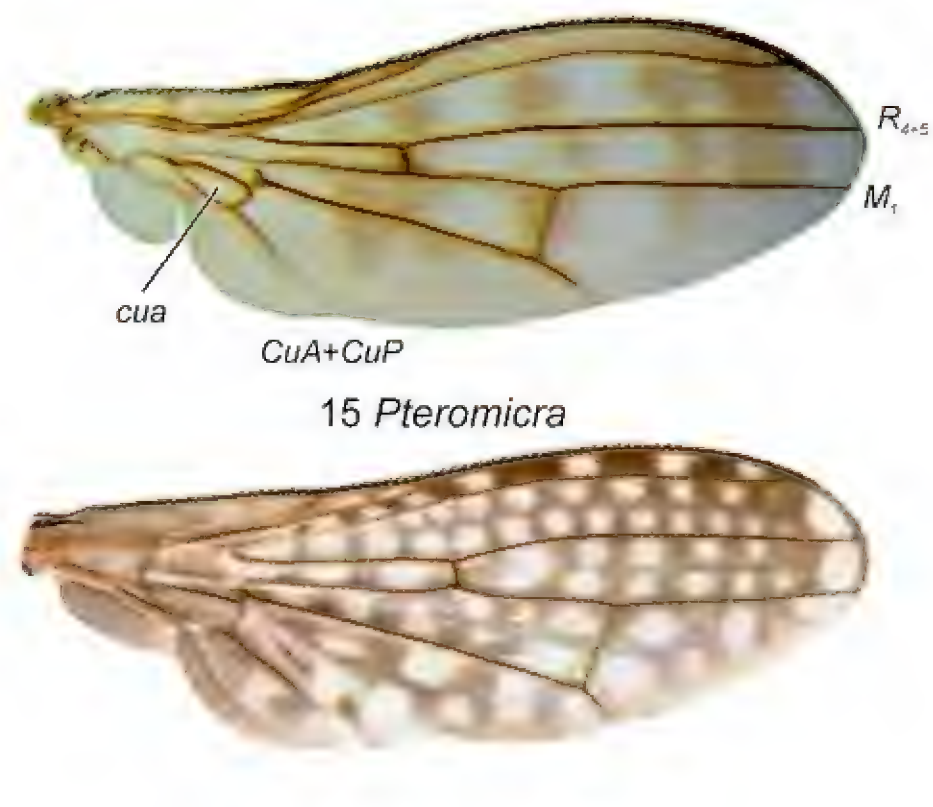


12 Sciomyzidae

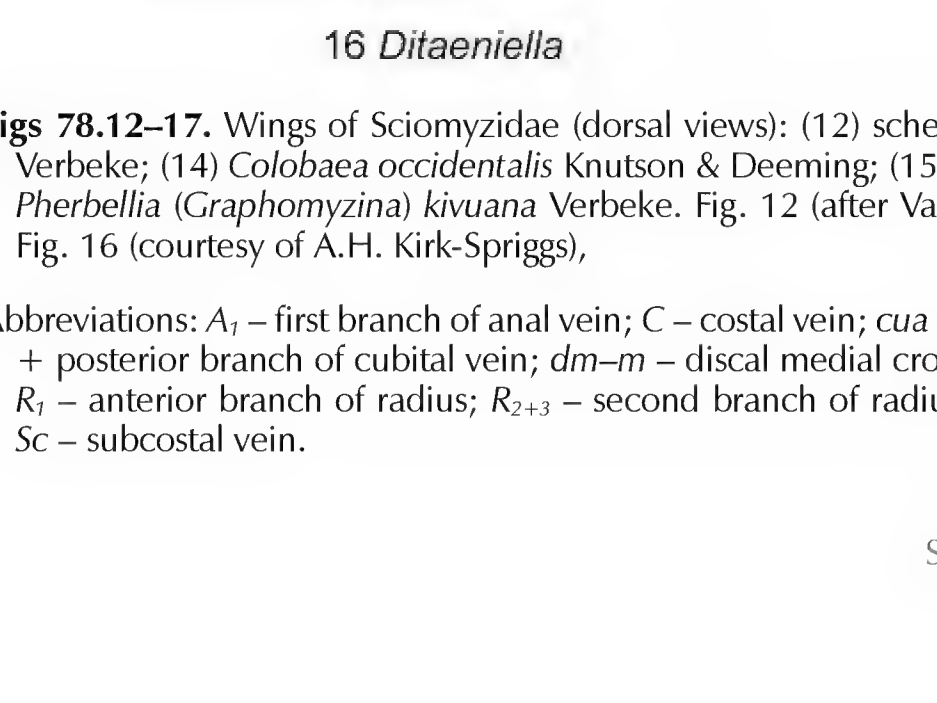
13 *Salticella*



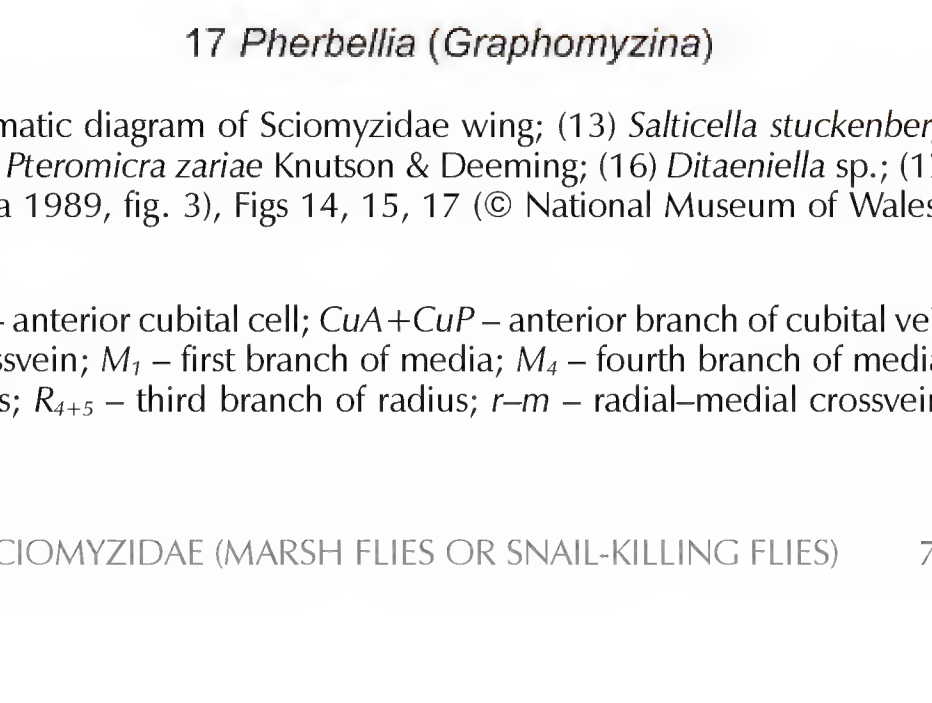
14 *Colobaea*



15 *Pteromicra*



16 *Ditaeniella*



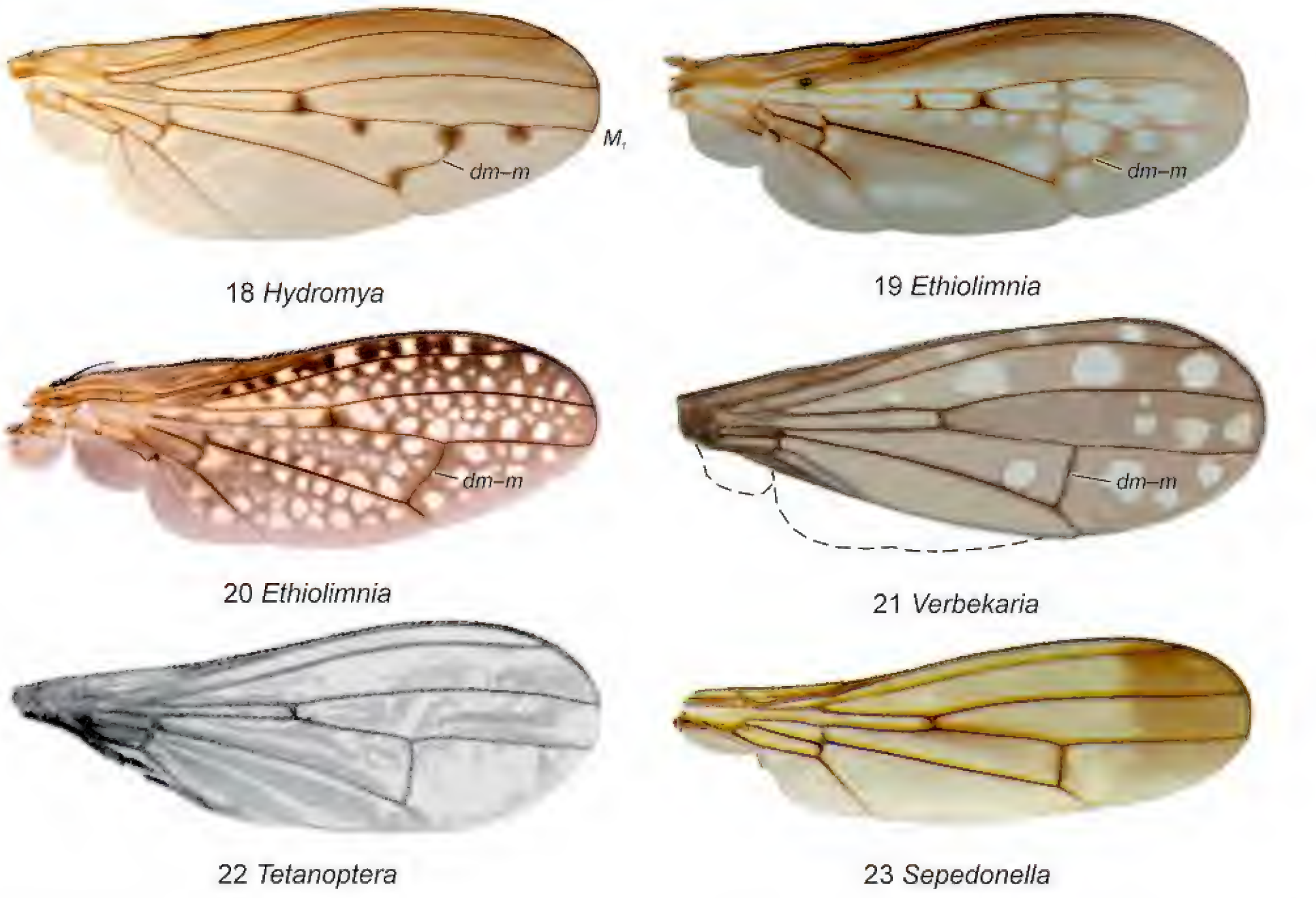
17 *Pherbellia* (*Graphomyzina*)

Figs 78.12–17. Wings of Sciomyzidae (dorsal views): (12) schematic diagram of Sciomyzidae wing; (13) *Salticella stuckenbergi* Verbeke; (14) *Colobaea occidentalis* Knutson & Deeming; (15) *Pteromicra zariae* Knutson & Deeming; (16) *Ditaeniella* sp.; (17) *Pherbellia* (*Graphomyzina*) *kivuana* Verbeke. Fig. 12 (after Vala 1989, fig. 3), Figs 14, 15, 17 (© National Museum of Wales), Fig. 16 (courtesy of A.H. Kirk-Spriggs),

Abbreviations: A_1 – first branch of anal vein; *C* – costal vein; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *dm–m* – discal medial crossvein; M_1 – first branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Sc* – subcostal vein.

(2004: 182) distinguished nine eco-groups. They applied 30 characters (of 37 genera): larval prey range, feeding behaviour, egg morphology and deposition sites, habitat, larval micro-habitat and larval morphology. They mapped the dispersion of the eco-groups onto a cladogram, based on a re-analysis of the characters in the first phylogenetic analysis by Marinoni & Mathis (2000).

Evolution of behaviour within a large, diverse genus of Sciomyzidae, with emphasis on feeding behaviour, micro-habitat and associated larval morphology, has been most extensively studied in the non-Afrotropical genus *Tetanocera* Duméril (39 Holarctic, Nearctic and Oriental species), species of which occur in various aquatic, shoreline and terrestrial habitats, by Chapman *et al*. (2006, 2012). Their phylogenetic analysis was based on their own DNA studies and the extensive studies of biology and morphology of immature stages by Foote (1996*a*, *b*, 2008, 2011, 2013, 1999). Chapman *et al*. (2006, 2012) concluded that larval habitat changes were robustly linked to larval pigmentation, float hair length, posterior spiracular disc orientation and spiracular disc ventrolateral lobe length. They speculated that terrestrial habitat preference and the morphological characters typical of terrestrial *Tetanocera* species all arose independently at least three times from the initial aquatic state and that the three subclades are distinct, each containing at least one aquatic and one terrestrial species. Chapman *et al*. (2012) showed the evolution of feeding behaviours and habitat changes in the Tetanocerini in a diagram. Their results strongly support a terrestrial ancestor for Sciomyzidae. They speculated that: 1) the evolution of aquatic larvae occurred relatively early in Tetanocerini phylogenesis; 2) from this ancestor, independent evolutionary reversals to terrestrial existence occurred in at least 10 lineages and that during the procedure there were at least 15 feeding behaviour transitions; 3) the ancestor of *Tetanocera* was a general predator of non-operculate snails, occurring just below the water surface; and 4) a minimum of five *Tetanocera* lineages made independent, evolutionary reversals to terrestrial existence, during which at least seven transitions in feeding behaviour occurred. They rejected the monophyly of some genera of sciomyzid predators of terrestrial snails and supported the hypothesis of multiple, independent transitions from aquatic shoreline to terrestrial predation within the Tetanocerini. They noted in their abstract (p. 15) "Transitioning from aquatic to terrestrial habitats is likely easier



Figs 78.18–23. Wings of Sciomyzidae (dorsal views): (18) *Hydromya dorsalis* (F.) (non-Afrotropical); (19) *Ethiolimnia lindneri* Verbeke; (20) *E. geniculata* (Loew); (21) *Verbekaria punctipennis* Knutson; (22) *Tetanoptera leucodactyla* Verbeke; (23) *Sepedonella nana* Verbeke. Fig. 22 (photographs © O. Lonsdale).

Abbreviations: *dm–m* – discal medial crossvein; M_1 – first branch of media.

than the reverse for sciomyzids because morphological characters associated with air-breathing while under the water's surface are lost rather than gained..." and they included a paragraph long section (p. 15) entitled "Sciomyzids violate trends in habitat transitions."

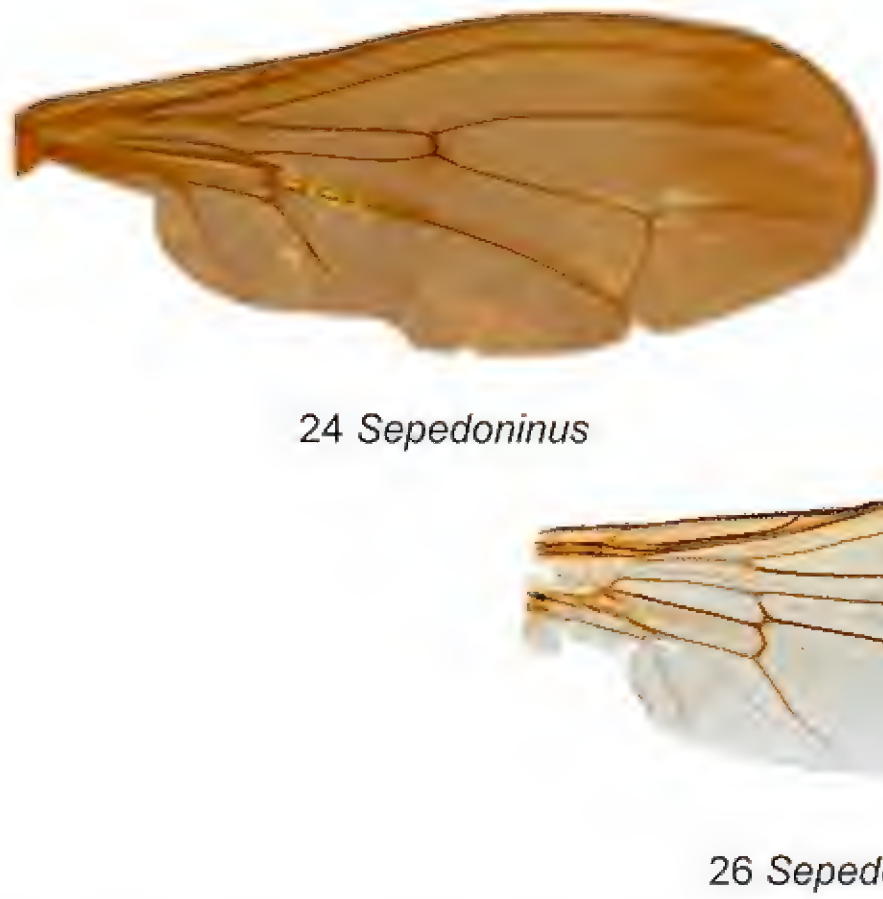
The life histories of Sciomyzidae include various phenological types that were established by Berg *et al*. (1982: 26) with five distinct groups (1–5) and extended by Vala (1989: 26), who included a new group (5a). All groups are based on multivoltine/univoltine aspects and overwintering stages (egg, larva, puparium or adult), with or without diapause. In addition, Gbedjissi (2003) described a new group for the multivoltine Afrotropical sciomyzids, based on absence of diapause, presence of mature adults throughout the year and higher population during periods of precipitation and lower populations during warm periods. Later, Barker *et al*. (2004: 189), suggested a similar specific group (group 6) for the multivoltine species in warm temperate and tropical areas, characterised by reproduction throughout the year and a lack of diapause, which appears typical for Afrotropical sciomyzids. Knutson & Vala (2011) widely applied this phenological group for species in tropical regions.

Economic significance

Berg (1953) first confirmed malacophagous feeding for the larvae of several species. Since then, their potential application as biological control agents against undesirable snails and slugs in agriculture, or of snails as intermediate hosts of trematode parasites of humans and livestock, has been pursued. Details on field trials and laboratory mass rearings have been summarised by Barker *et al*. (2004: 194), Knutson & Vala (2011: 400) and Murphy *et al*. (2012).

Chock *et al*. (1961) made the first field introduction of an exogenous species, *i.e.*, *Sepedomerus macropus* (Walker, 1849) from Nicaragua, into one of the Hawaiian islands, for control of the freshwater snail host of the liver fluke, *Fasciola gigantica* Cobbold (Fasciolidae), which attacks cattle. The sciomyzid became well-established and has dispersed to other Hawaiian islands, but its impacts have not been determined. Tirgari (1977) and Tirgari & Massoud (1981), released many individuals of the endemic *Sepedon* (*Sepedon*) *sphegea* (F., 1775) in rice paddies in Iran and noted after 15 days a reduction of 76–94% (in water 4.0 cm deep) and 48–85% (in water 30 cm deep) of the population of the aquatic snail *Bulinus truncatus* (Audouin) (Planorbidae), which is involved in the transmission of human schistosomiasis.

In sub-Saharan Africa (mainly in Benin and South Africa), studies by several researchers have been conducted in the laboratory and in nature to determine the effectiveness of some sciomyzids for control of freshwater snails that are intermediate hosts of *Schistosoma haematobium* (Bilharz) and *S. mansoni* Sambon (Schistosomatidae), causing schistosomiasis of humans. Experiments were carried out with the autochthonous intermediate host snails *Biomphalaria pfeifferi* (Krauss) (Planorbidae), *Bulinus africanus* (Krauss), *B. tropicus* (Krauss), *Indoplanorbis exustus* (Deshayes) (Planorbidae), *Radix natalensis* (Krauss) (Lymnaeidae) and species of *Sepedon* (*Parasepedon* Verbeke) (Sciomyzidae) collected in the endemic areas of these diseases. Some allochthonous species, *i.e.*, *Biomphalaria glabrata* Say (Planorbidae) and *Physella acuta* (Draparnaud) (Physidae) were tested alone, or in association with native snail prey. Maharaj (1991) showed that larval predation by *S.* (*P.*) *scapularis* of *B. tropicus* increased in relation to snail density. This density dependency was, however, not observed using *S.* (*P.*) *neavei* larvae. Maharaj *et al*. (1992) suggested that *S.* (*P.*) *scapularis* was an efficient predator of *B. africanus* and *B. tropicus* and could be a good candidate as a



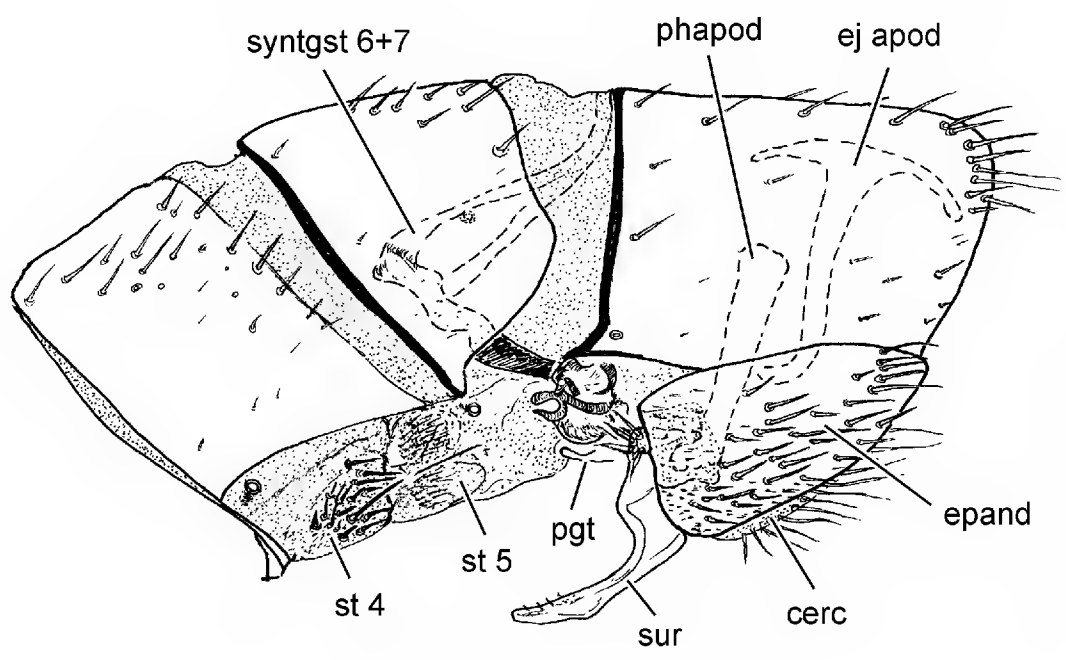
Figs 78.24–26. Wings of Sciomyzidae (dorsal views): (24) *Sepedoninus curvisetis* Verbeke; (25) *Sepedon* (*Parasepedon*) *ruficeps* Becker; (26) *S.* (*P.*) *saegeri* Verbeke.

biological control agent against these snails. They confirmed the influence of the size of the snail prey on the level of predation. Appleton *et al*. (1993) estimated a daily production of 1,000 first-instar larvae by 30 females of *S*. (*P*.) *neavei* required to control *Schistosoma*. They recognised eight criteria required for the selection of a potential agent. These authors specified some consumption and prey preference aspects of *S*. (*P*.) *ruficeps* larvae, as had Gbedjissi *et al*. (2003). For this species, Gbedjissi & Vala (2014) found that the larvae of *S*. (*P*.) *neavei* attacked significantly more *Biomphalaria pfeifferi* infected with *Schistosoma* than they attacked *Bulinus globosus* infested with *Shistosoma*. There is an extensive literature on the above and related aspects of other sciomyzids and their gastropod hosts/prey summarised and analysed by Agboho (2018), Barker *et al*. (2004: 176), Knutson & Vala (2011: 72) and Murphy *et al*. (2012).

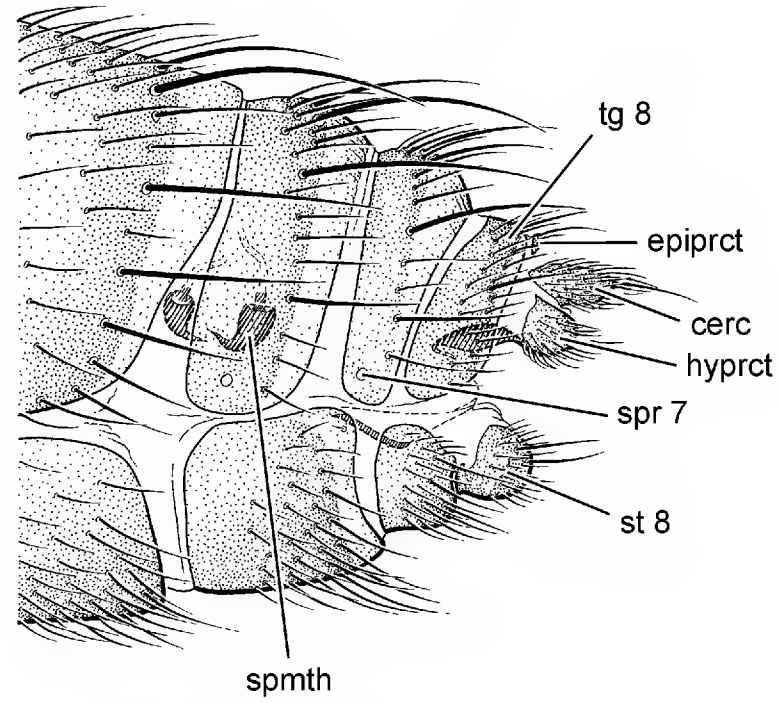
Biocontrol by the Afrotropical *Sepedon* (*P*.) *umbrosa* was tested in nature against the terrestrial mollusc *Subulina octona* (Bruguière) (Subulinidae), which feeds on various greenhouse, agricultural and garden plants. Their larvae attack this snail in Benin; they are parasitoids at first by penetrating directly into the mouth opening (56.25%) or into the pallial cavity near the pneumostomal opening (43.75%) and become saprophages later (Gbedjissi 2003; Gbedjissi *et al*. 2020).

Classification

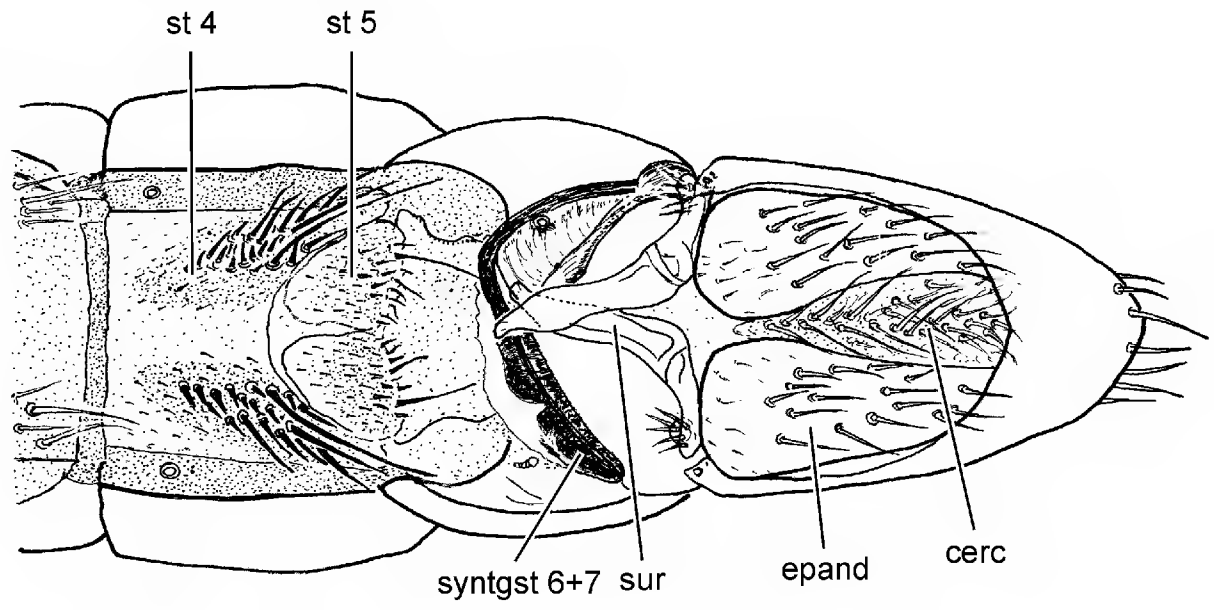
The Sciomyzidae is one of the families of the Acalyptratae superfamily Sciomyzoidea proposed by Hendel (1916), who included the Clusiidae, Coelopidae, Sciomyzidae and the



27 *Tetanoptera* ♂



29 *Tetanocera* ♀



28 *Tetanoptera* ♂

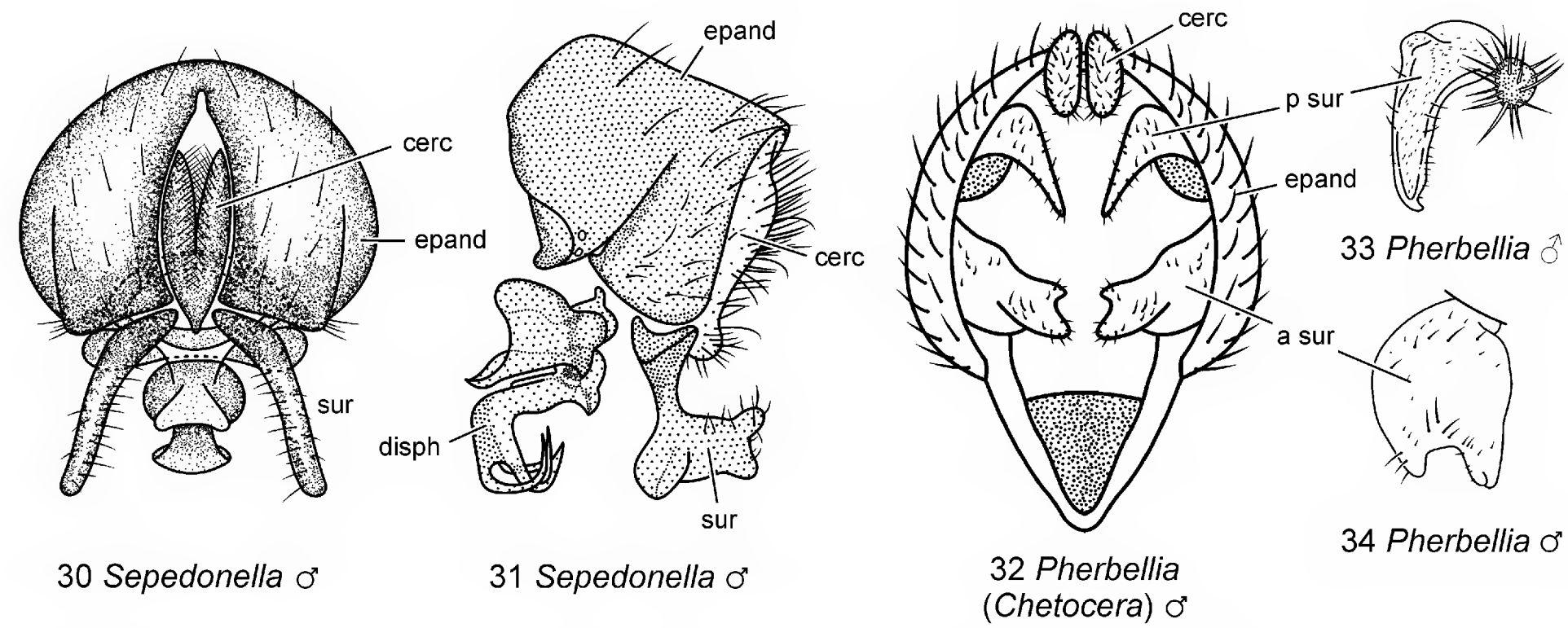
Figs 78.27–29. Male and female terminalia of Sciomyzidae: (27) male postabdomen of *Tetanoptera leucodactyla* Verbeke, lateral view; (28) same, ventral view; (29) female postabdomen of *Tetanocera plebeja* Loew, lateral view (non-Afrotropical). Figs 27, 28 (Knutson & Vala 1999, figs 3, 4a), Fig. 29 (Knutson 1987, fig. 20).

Abbreviations: cerc – cercus; ej apod – ejaculatory apodeme; epand – epandrium; epiprct – epiproct; hyprct – hypoproct; pgt – postgonite; phapod – phallapodeme; spmth – spermatheca; spr – spiracle; st – sternite; sur – surstylus; syntgst – syntergosternite; tg – tergite.

non-Afrotropical families Dryomyzidae, Neottiophilidae and Ropalomeridae. The Neottiophilidae were included as a subfamily of Piophilidae (Tephritoidea) and the Clusiidae in the Opomyzoidea by McAlpine (1989: 1504). Hennig (1958) included the families Coelopidae, Sciomyzidae, Sepsidae and the non-Afrotropical families Dryomyzidae, Helcomyzidae and Ropalomeridae, in Sciomyzoidea, but did not mention non-Afrotropical *Pelidnoptera* Rondani or Phaeomyiidae. McAlpine (1989: 1504) included those families, but placed Helcomyzidae in the Dryomyzidae, added Helosciomyzidae and placed Phaeomyiinae (tentatively) as a subfamily of Sciomyzidae. Barraclough & McAlpine (2006) described the new family Natalimyzidae, based on a new genus and species from South Africa. They placed it as *incertae sedis* in the "wider Sciomyzoidea", *i.e.*, the Sciomyzoidea + Lauxanioidea of McAlpine (1991*a*, *b*). They discussed its relationships to the superfamilies of Schizophora, especially in regard to the wider Sciomyzoidea and noted (p. 133), "... no definite sister group relationship ..." could be determined. The number of Sciomyzoidea families increased by the addition of Helcomyzidae, Heterocheilidae (as a new family), Huttoninidae and all families of the Lauxanioidea (McAlpine 1991*a*, *b*). McAlpine (1989: 1504) considered the Lauxanioidea as a separate superfamily, but Colless & McAlpine (1970: 678, 1991: 768) placed the Lauxanioidea families in the Sciomyzoidea. Later a species of the family Natalimyzidae from Baltic amber was described by Tschirnhaus & Hoffeins (2009). Based on a detailed study of aspects of antennal morphology in Diptera (181 figures), McAlpine (2011) retained the Lauxanioidea families in the Sciomyzoidea and further assessed McAlpine's reasons for separating the two superfamilies.

Speight (1969: 336) stated that "The taxonomic concept 'Sciomyzoidea' seems to have arisen as a result of disintegration of earlier, ... ill-defined family groups ... and that Hennig's (1958) ... justification ... is tortuous." Hennig (1971) included the same families as in his 1958 classification and tentatively added the non-Afrotropical Eurychoromyiidae. He extensively commented on Speight (1969), with whose methods of analysis he somewhat disagreed. McAlpine (1989: 1449) characterised the Sciomyzoidea as "... one of the least contentious of all superfamilies of Acalyptratae." Meier (1996: 26) commented that the Sciomyzoidea is a "... problematic taxon within the acalyptrate flies" and Barraclough & McAlpine (2006: 131) noted, "... the limits of the Sciomyzoidea are not agreed upon ... sciomyzoid families are associated together largely because they span a gradation of character state combinations ..." The "tortuous" taxonomic/phylogenetic/nomenclatorial history of Sciomyzoidea was discussed to some extent by Berg & Knutson (1978) and Knutson & Vala (2011: 340).

In their phylogenomic estimate of fly relationships, based on molecules from 149 of 157 families of Diptera, Wiegmann *et al*. (2011) recovered five of the superfamilies of Acalyptratae (including Sciomyzoidea), "... with minor modifications ..." (p. 26). The Sciomyzoidea were the sister-group to Lauxanioidea and included all of the above-mentioned families, plus Huttoninidae, except Ropalomeridae and Sepsidae were excluded. Wiegmann *et al*. (2011) did not cite Gibson *et al*. (2010), which was the first attempt to phylogenetically place Conopidae using molecular characters, as well as the most extensive molecular analysis of relationships within Schizophora (Diptera) to that date. Sciomyzoidea was not included among the seven acalyptrate superfamilies they analysed. In Gibson *et al*.'s (2010) parsimony analysis, Conopidae were placed as sister to the remaining Schizophora and their Bayesian analysis recovered a Conopidae + Lauxaniidae clade. Tóthová *et al*. (2012: 2) commented in reference to Wiegmann *et al*. (2011), "... Conopidae might also be included in Sciomyzoidea, but



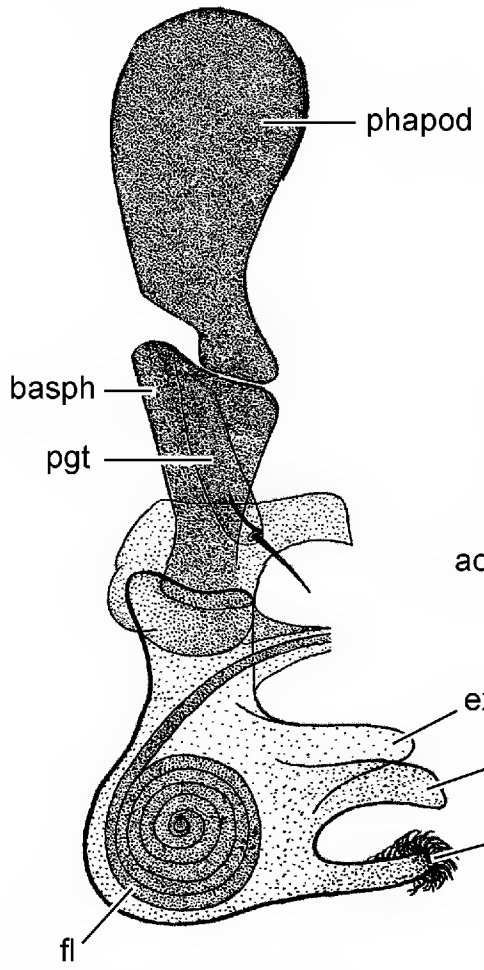
Figs 78.30–34. Male terminalia of Sciomyzidae: (30) hypopygium of *Sepedonella nana* Verbeke, posterior view; (31) same, *S. castanea* Knutson & Deeming, lateral view; (32) same, *Pherbellia* (*Chetocera*) *obtusa* (Fallén), ventral view (non-Afrotropical); (33) same, surstylus, posterior view; (34) same, anterior view. Fig. 30 (after Verbeke 1950, fig. 78); Fig. 31 (after Knutson *et al*. 2018, fig. 27); Figs 32–34 (after Vala 1989, figs 38a, b, c).

Abbreviations: a sur – anterior surstylus; cerc – cercus; distph – distiphallus; epand – epandrium; p sur – posterior surstylus; sur – surstylus.

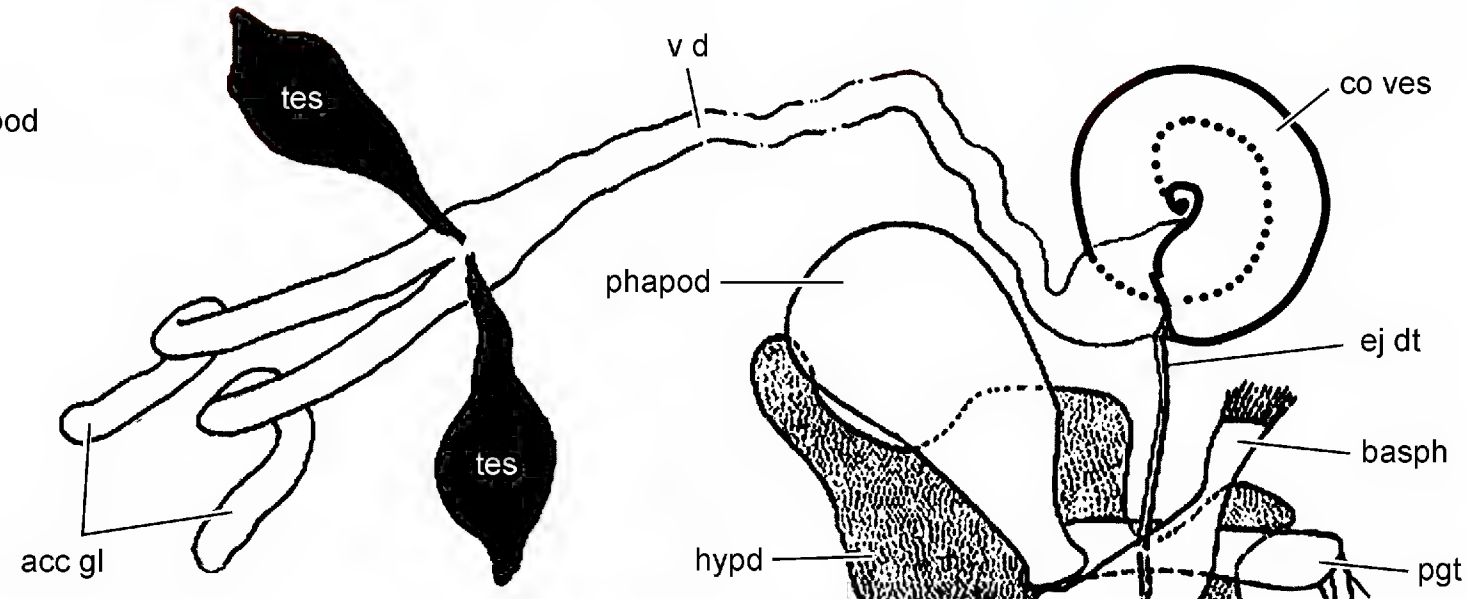
35 *Sepedon* (*Parasepedon*) ♂

36 *Sepedon* (*Parasepedon*) ♂

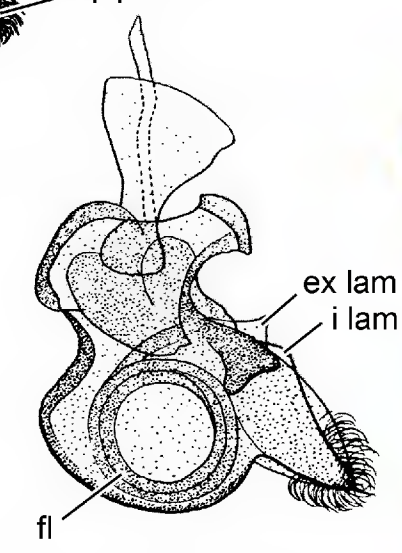
37 *Sepedon* (*Parasepedon*) ♂



39 *Sepedon* (*Parasepedon*) ♂



38 *Sepedon* (*Parasepedon*) ♂



40 *Sepedon* (*Parasepedon*) ♂

41 *Sepedon* (*Parasepedon*) ♂

42 *Sepedon* (*Parasepedon*) ♂

Figs 78.35–42. Male terminalia of Sciomyzidae: (35) surstyli of *Sepedon* (*Parasepedon*) *senegalensis* Macquart, ventral view; (36) same, *S.* (*P.*) *notambe* Verbeke; (37) same, *S.* (*P.*) *schoutedeni* Verbeke; (38) genital tract, hypandrium and phallus of *S.* (*P.*) *senex* Wiedemann, lateral view; (39) hypandrium and phallus of *S.* (*P.*) *lippensi* Verbeke; (40) phallus of *S.* (*P.*) *simulans* Verbeke, lateral view; (41) same, *S.* (*P.*) *senegalensis* Macquart; (42) cochleate vesicle of *S.* (*P.*) *trichrooscelis* Speiser, lateral view. Figs 35–37, 41, 42 (photographs © S. Hanot), Fig. 38 (Steyskal & Knutson 1975, fig. 2), Figs 39, 40 (after Verbeke 1961, figs 4, 17).

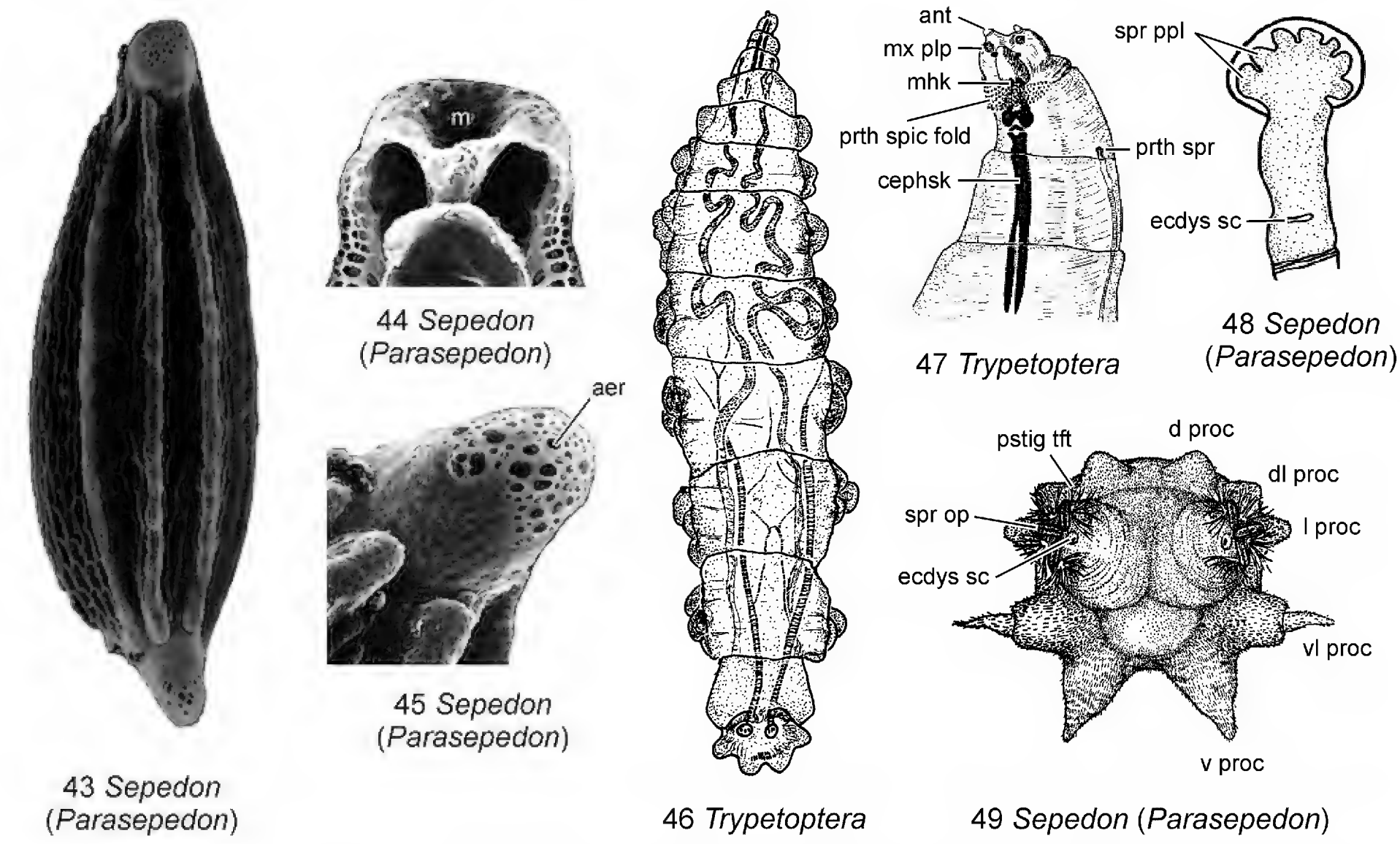
Abbreviations: acc gl – accessory gland; basph – basiphallus; co ves – cochleate vesicle; distph – distiphallus; ej dt – ejaculatory duct; epiph – epiphallus; ex lam – external lamella; fl – filament; hypd – hypandrium; i lam – internal lamella; pgt – postgonite; phapod – phallapodeme; tes – testis; v d – vas deferens.

this proposal needs further study …" and concluded that "The present concept of Sciomyzoidea (*i.e.*, Wiegmann *et al*. 2011) thus includes 11 families" (all of those listed above). However, their inclusion of reference to McAlpine (1991*a*, *b*) and Barraclough & McAlpine (2006) is an error, as the last three mentioned publications also include the families of Lauxanioidea in the wider Sciomyzoidea. Furthermore, in their analysis Tóthová *et al*. 2012 placed non-Afrotropical *Pelidnoptera* (Phaeomyiidae of authors) in the subfamily Phaeomyiinae of Sciomyzidae.

The nomenclature of Sciomyzidae has been gradually changed and refined since the first species description, *i.e.* the Palaearctic *Musca umbrarum* L., 1758, later placed in *Dictya* by Meigen (1803). Until recently, all classifications and identification keys were based on characters of adults. Fallén (1820: 1) created the family Sciomyzides with *Dryomyza* Fallén, *Sciomyza* Fallén, *Sepedon* and *Tetanocera*. Schiner (1862) distinguished the subfamilies Sciomyzinae and Tetanocerinae. Macquart (1846) first used the term Sciomyzidae (= Tetanoceridae Macquart). Hendel (1924) added the subfamily Tetanurinae and the tribe Salticellini, which Séguy (1934: 295), raised to the rank of subfamily (Salticellinae). Barnes (1979, 1981), Griffiths (1972: 173), Hennig (1958, 1965, 1971), D.K. McAlpine (1991*b*, 1992), J.F. McAlpine (1963, 1989: 1449), Steyskal (1965) and Verbeke (1950) reviewed the suprageneric and subfamilial classifications of Sciomyzidae and some of the related families within the Sciomyzoidea, especially "Phaeomyiidae," the status of which has been discussed often (see below).

Verbeke (1950), basing his evaluation on the circumvolution and symmetry/asymmetry of the postabdomen of males, proposed a new subfamily classification in regard to Afrotropical and Palaearctic genera: Renocerinae, Sciomyzinae (with Phaeomyiina as a new subtribe), Sepedoninae and Tetanocerinae. Steyskal (1965), in regard to the morphology of adults, distinguished five suprageneric groups globally: Helosciomyzinae (Australia and New Zealand), Huttonininae (New Zealand), Phaeomyiinae (Palaearctic), Salticellinae (Palaearctic + South Africa), and Sciomyzinae (tribes Sciomyzini and Tetanocerini, virtually cosmopolitan).

Hennig (1965), in reviewing the classifications of Steyskal (1965) and Verbeke (1950), recognised nine subfamilies:

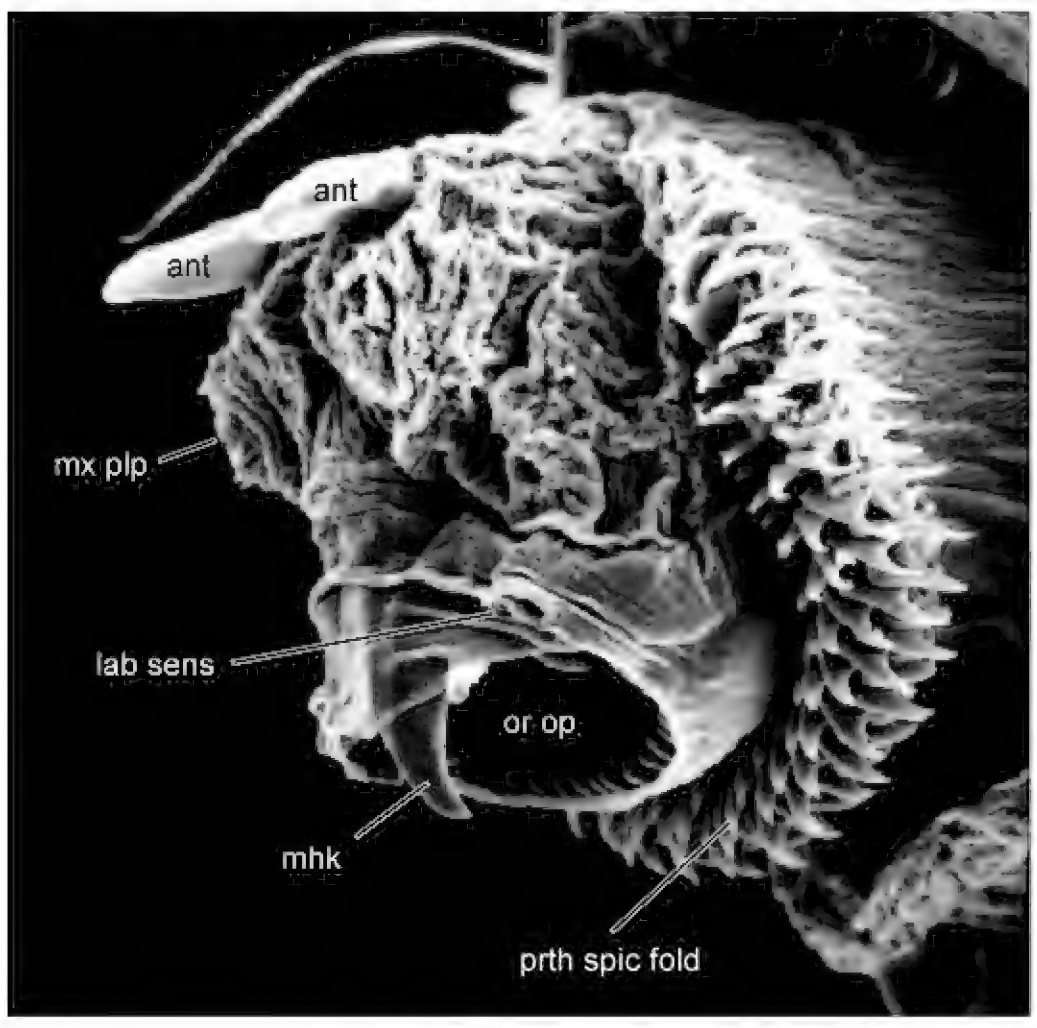


Figs 78.43–49. Immature stages of Sciomyzidae: (43) egg of *Sepedon* (*Parasepedon*) *trichrooscelis* Speiser, dorsal view; (44) same, anterior view; (45) same, caudal view; (46) habitus of third-instar larva of *Trypetoptera punctulata* (Scopoli), dorsal view (non-Afrotropical); (47) same, anterior end, ventrolateral view; (48) prothoracic spiracles of *S.* (*P.*) *trichrooscelis*, lateral view; (49) posterior spiracular plate of third-instar larva of *S.* (*P.*) *ruficeps* Becker, posterior view. Figs 44, 48 (Vala & Gbedjissi 1995, figs 4, 30), Figs 46, 47 (Vala 1986, figs 17, 18), Fig. 48 (Vala *et al*. 1995, fig. 30), Fig. 49 (Knutson *et al*. 1967, fig. 4).

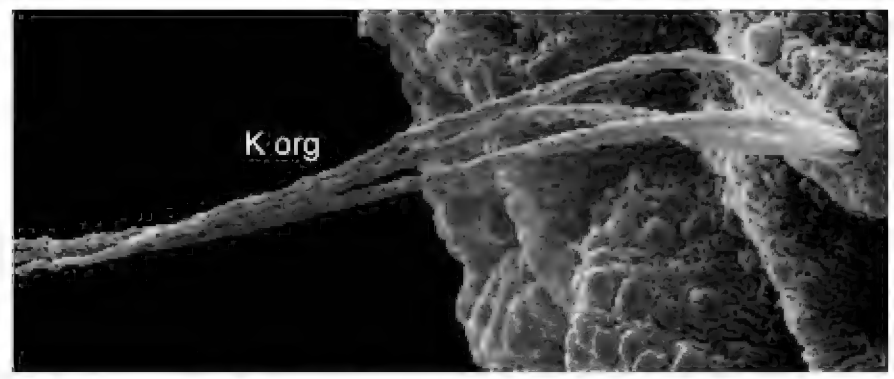
Abbreviations: aer – aeropyle; ant – antenna; cephsk – cephaloskeleton; d proc – dorsal process; dl proc – dorsolateral process; ecdys sc – ecdysial scar; l proc – lateral process; m – micropore; mhk – mouthhook; mx plp – maxillary palpus; prth spic fold – prothoracic spiculate fold; prth spr – prothoracic spiracle; pstig tft – peristigmatic tuft; spr op – spiracular opening; spr ppl – spiracular papillae; v proc – ventral process; vl proc – ventrolateral process.

Helosciomyzinae, Huttonininae, Neolimininae (?), Phaeomyiinae, Renocerinae, Salticellinae, Sciomyzinae, Sepedoninae and Tetanocerinae, at least tentatively. Griffiths (1972: 174), on the basis of adult characters, erected two previously proposed entities as distinct families: Helosciomyzidae (including Huttonininae) and Phaeomyiidae. Barnes (1979, 1981) excluded Huttonininae, on the basis of morphological characters of larvae. McAlpine (1989: 1452) retained the four subfamilies Huttonininae, Phaeomyiinae, Salticellinae and Sciomyzinae. Vala (1989) concluded that the Sciomyzidae includes only the subfamilies Phaeomyiinae, Salticellinae and Sciomyzinae. Vala *et al*. (1990) agreed with the proposal of Griffiths (1972: 174), regarding "Phaeomyiidae", based on larval morphologies and non-malacophagous feeding, thus following Griffiths' (1972: 173) suggestion that the Phaeomyiidae are a distinct family "… if their larvae and larval development were other than those of sciomyzids …" Knutson & Vala (2011: 338) discussed the supra-generic classifications and phylogeny. They distinguished the three subfamilies Huttonininae, Salticellinae and Sciomyzinae (the last-named subfamily divided into the tribes Sciomyzini and Tetanocerini). The Phaeomyiidae (with two genera and five species) were considered as a sister-group to the Sciomyzidae. In recent years, the study of Sciomyzidae has included data from phylogenetic analyses, larval morphology, life cycle studies and molecular aspects. From DNA studies, notable advancements have been obtained in regard to the phylogenetic relationships among Salticellinae, Sciomyzinae (Sciomyzini and Tetanocerini) and the rank of the "Phaeomyiidae" (based on *Pelidnoptera*) as a sister-group or not of the Sciomyzidae and in the evolution of the larval feeding behaviours.

Marinoni & Mathis (2000) included two larval and 36 adult characters of the type species of 50 of the 63 known genera for the first phylogenetic analysis of genera. They considered Phaeomyiidae as sister-group to the Sciomyzidae (Salticellinae + Sciomyzinae), concluding that the two tribes of Sciomyzinae were monophyletic, but found a large number of genera in polytomies. Barker *et al*. (2004: 172) reworked this study, omitted larval characters and added seven new adult characters (chaetotaxy, wing venation and hind femur shape). Among these studies, the overall trees are consistent with the *Teutoniomyia* Hennig to *Sepedonea* Steyskal lineage, located at the terminus of their cladograms. Both analyses attested to the monophyly of the family (Salticellinae + Sciomyzinae) and the monophyly of the two tribes of the Sciomyzinae. There are significant differences, however, in location of a number of taxa in these trees; notably, seven genera placed as higher Tetanocerini by Marinoni & Mathis (2000) appear at the base of the Tetanocerini in Barker *et al*. (2004: 172). These two studies included all of the



50 *Sepedon* (*Sepedon*)



51 *Sepedon* (*Mesosepedon*)

52 *Sepedon* (*Parasepedon*)

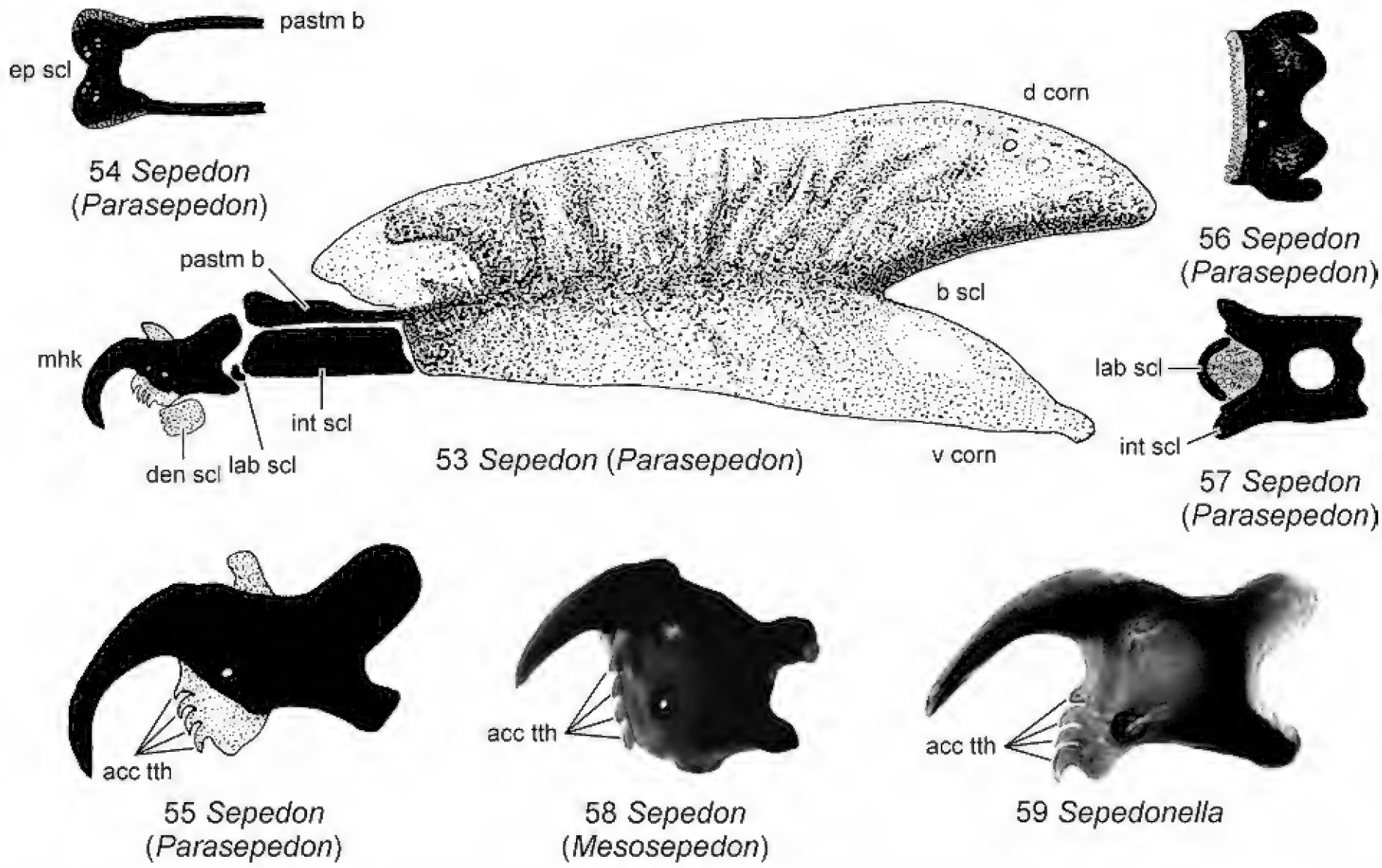
Figs 78.50–52. Stereoscan micrographs of immature stages of Sciomyzidae: (50) pseudocephalon and segment 1 of third-instar larva of *Sepedon* (*Sepedon*) *sphegea* (F.), anterolateral view (non-Afrotropical); (51) larval Keilin's organ of *S*. (*Mesosepedon*) *knutsoni* Vala, Gbedjissi & Dossou, ventral view; (52) third-instar larva of *S*. (*Parasepedon*) *trichrooscelis* Speiser, ventrolateral view. Fig. 50 (Vala & Rougon 2008, fig. 3b).

Abbreviations: ant – antenna; K org – Keilin's organ; lab sens – labial sensilla; mhk – mouthhook; mx plp – maxillary palpus; or op – oral opening; prth spic fold – prothoracic spiculate fold; pstig tft – peristigmatic tuft; v proc – ventral process; vl proc – ventrolateral process.

genera occurring in the Afrotropical Region, except *Ditaeniella* Sack and *Verbekaria* Knutson. The "*Sepedon* group of genera" – *Sepedon*, *Sepedonea*, *Sepedonella* Verbeke, *Sepedoninus*, *Sepedomerus* Steyskal and *Thecomyia* Perty, plus possibly *Ethiolimnia* Verbeke and *Teutoniomyia* – appear to be the most corroborated lineage, according to the phylogenetic studies of Barker *et al*. (2004: 172) and Marinoni & Mathis (2000).

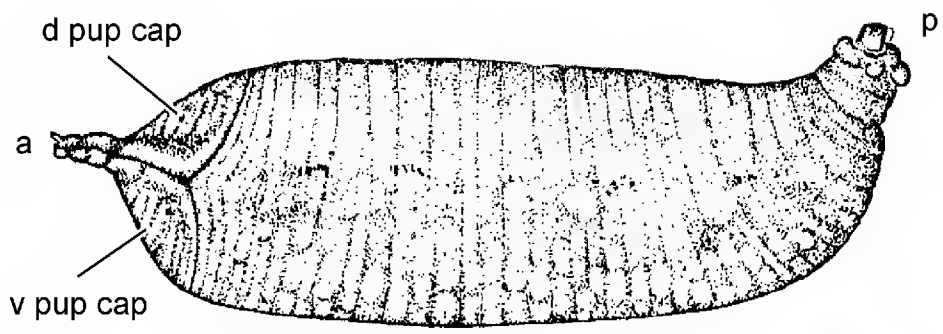
The Tetanocerini, especially *Tetanocera*, is the most thoroughly analysed supra-generic category in regard to phylogenetic relationships and evolutionary tracks, as based on modern methods (Chapman *et al*. 2006, 2012; Tóthová *et al*. 2012). Chapman *et al*. (2012) applied Bayesian inference and maximum likelihood to analyse a concatenated 5-gene data set (mitochondrial loci COI, COII, 16S and nuclear loci 28S, EF-1α) of 64 Nearctic and Holarctic species of Sciomyzidae: two Sciomyzini (in two of the 13 genera), 62 Tetanocerini (19 of the 45 genera, including 34 species of *Tetanocera*) and one Phaeomyiidae (*Pelidnoptera nigripennis*), which they recognised as representing a family, but found it (in the Sciomyzidae) as the sister lineage to the Tetanocerini. They confirmed the monophyly of the suprageneric categories Sciomyzinae, Sciomyzini and Tetanocerini. They referred to *Akebono* Sueyoshi and *Pelidnoptera* as Phaeomyiidae in their text and tables. Both of their methods of phylogenetic analysis recovered *Pelidnoptera nigripennis* as the sister lineage to the Tetanocerini, suggesting its potential status as a tribe within the Sciomyzinae, but in their cladogram it was labelled "Phaeomyiidae". They noted that some genera, including many studied species, were also monophyletic, e.g., *Dictya*, *Elgiva* Meigen and *Sepedon*.

Tóthová *et al*. (2012) analysed phylogenetic relationships across the family, based on nucleotide sequences from the mitochondrial (12S, 16S, COI, COII, Cytb) and nuclear genomes (28S, EF1α) for 54 Holarctic and Palaearctic species of Sciomyzidae: 19 Sciomyzini (in five genera), 32 Tetanocerini (in 15 genera), one species of Salticellinae, two species of one genus of Phaeomyiinae and seven species of five other families of Sciomyzoidea (Coelopidae, Dryomyzidae, Helcomyzidae, Heteromyzidae and "Huttoninidae" (the last-named included by the authors in Sciomyzidae)) as outgroups. Their Bayesian, parsimony and likelihood analyses of the molecular data and of the combined molecular and adult morphological data (the latter data set from Barker *et al*. 2004), supported many

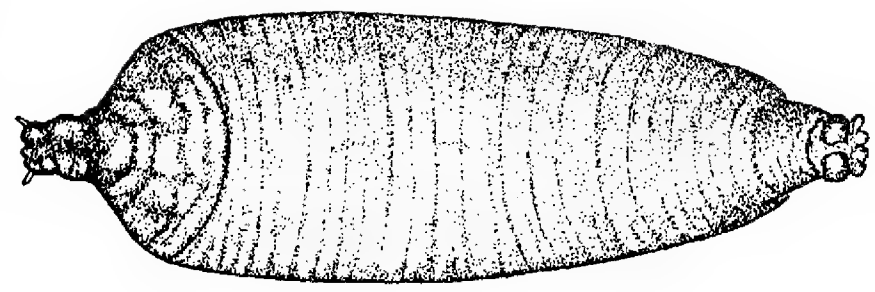


Figs 78.53–59. Immature stages of Sciomyzidae: (53) cephaloskeleton of third-instar larva of *Sepedon* (*Parasepedon*) *trichrooscelis* Speiser, lateral view; (54) same, epistomal sclerite and parastomal bars, dorsal view; (55) same, mouthhook, lateral view; (56) same, dental sclerite, ventral view; (57) intermediate sclerites, ventral view; (58) mouthhook of third-instar larva of *Sepedon* (*Mesosepedon*) *knutsoni* Vala, Gbedjissi & Dossou, lateral view; (59) same, *Sepedonella nana* Verbeke. Figs 53–57 (Vala *et al*. 1995, figs 32, 32A–D), Fig 59 (Vala & Gbedjissi 2011, fig.10A).

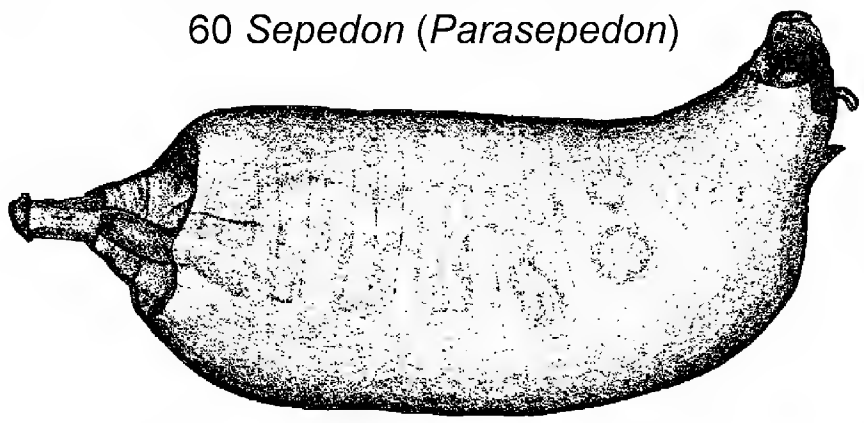
Abbreviations: acc tth – accessary teeth; b scl – basal sclerite; d corn – dorsal cornu; den scl – dental sclerite; ep scl – epistomal sclerite; int scl – intermediate sclerite; lab scl – labial sclerite; mhk – mouthhook; pastm b – parastomal bar; v corn – ventral cornu.



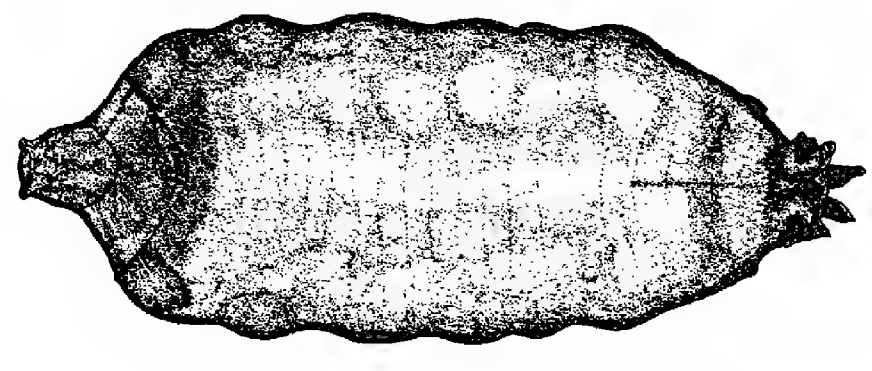
60 *Sepedon* (*Parasepedon*)



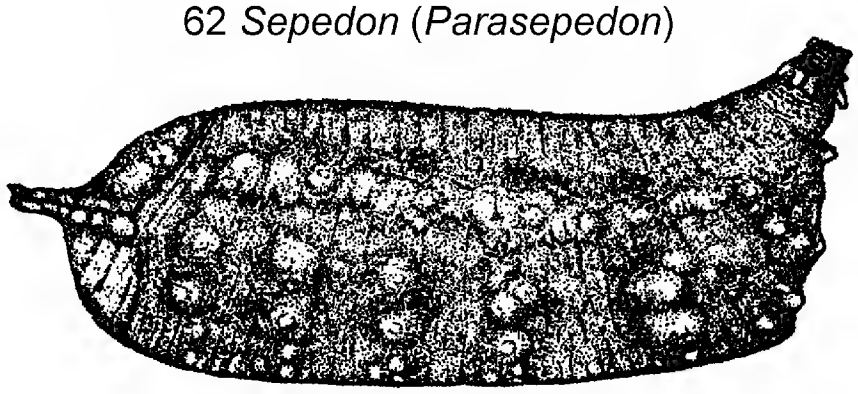
61 *Sepedon* (*Parasepedon*)



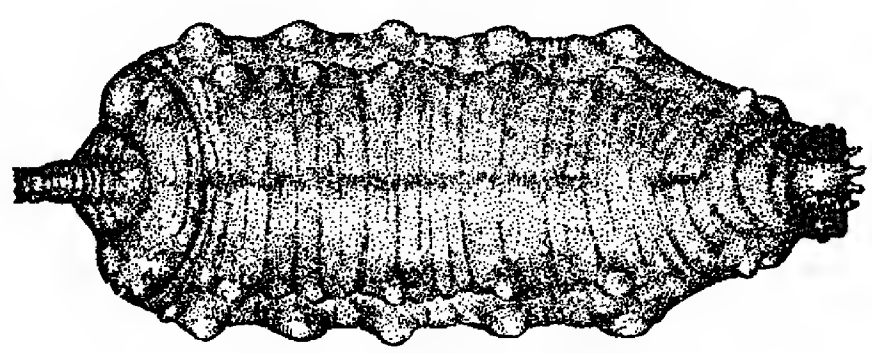
62 *Sepedon* (*Parasepedon*)



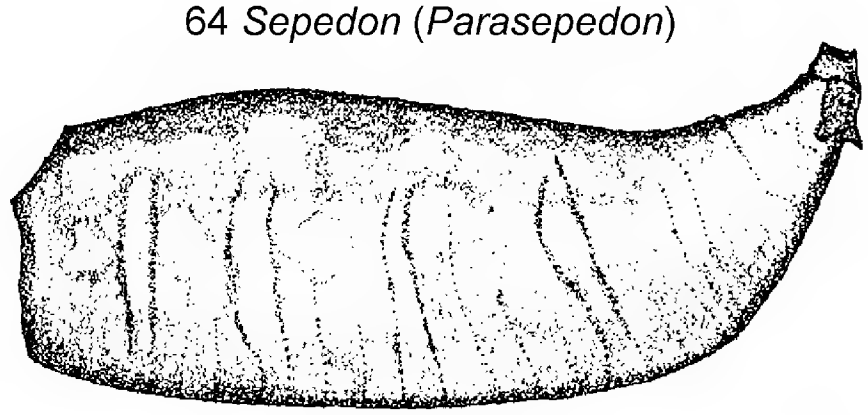
63 *Sepedon* (*Parasepedon*)



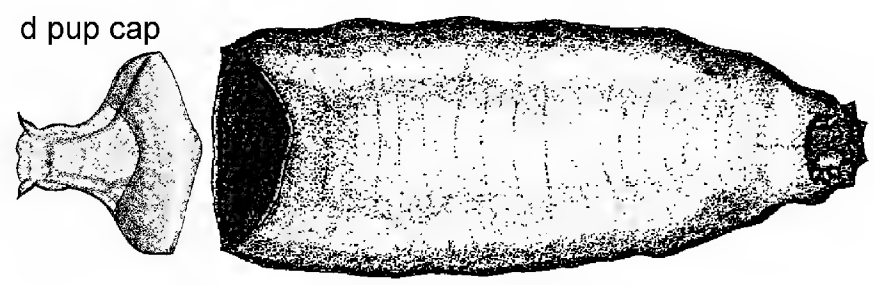
64 *Sepedon* (*Parasepedon*)



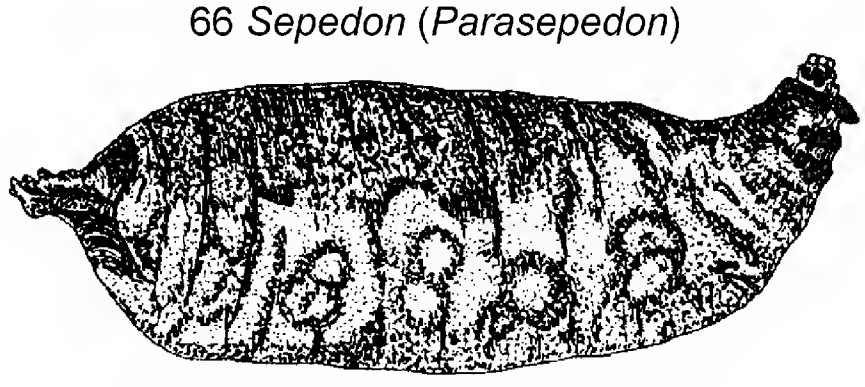
65 *Sepedon* (*Parasepedon*)



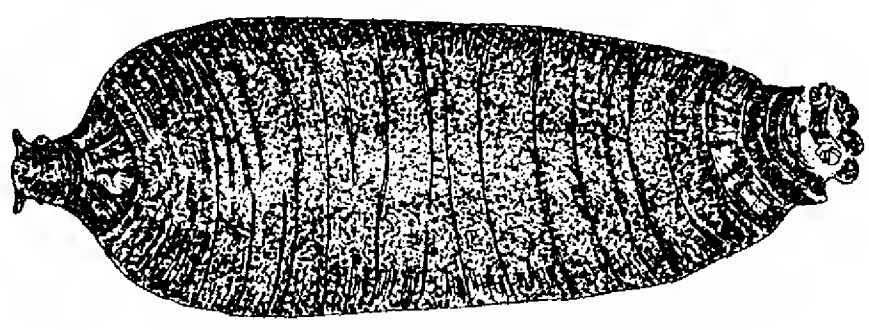
66 *Sepedon* (*Parasepedon*)



67 *Sepedon* (*Parasepedon*)



68 *Sepedon* (*Parasepedon*)



69 *Sepedon* (*Parasepedon*)

Figs 78.60–69. Immature stages of Sciomyzidae (puparia): (60) *Sepedon* (*Parasepedon*) *hispanica hispanica* Loew, lateral view; (61) same, dorsal view; (62) *S.* (*P.*) *neavei* Steyskal, lateral view; (63) same, dorsal view; (64) *S.* (*P.*) *ruficeps* Becker, lateral view; (65) same, dorsal view; (66) *S.* (*P.*) *testacea* Loew, lateral view (open); (67) same, puparial trunk, dorsal view (with detached dorsal puparial cap); (68) *S.* (*P.*) *trichrooscelis* Speiser, lateral view; (69) same, dorsal view. Figs 60, 61, 64, 65 (Knutson *et al*. 1967, figs 24, 23, 22, 21, respectively), Figs 62, 63, 66, 67 (Barraclough 1983, figs 30–34), Figs 68, 69 (Vala *et al*. 1995, figs 33, 34).

Abbreviations: a – anterior; d pup cap – dorsal puparial cap; p – posterior; v pup cap – ventral puparial cap.

results cited above. They confirmed the monophyly of the Sciomyzini and Tetanocerini and recovered five distinct clades within the Tetanocerini. They recovered the genus *Tetanocera*, based on seven of the 39 species, well-separated from other genera of Tetanocerini, as noted by Chapman *et al*. (2012). In agreement with taxonomic studies and the two previous trees based solely on adult morphology, they strongly confirmed the paraphyly of the genus *Pherbellia* Robineau-Desvoidy (therein based on 12 of the 97 currently recognised species), but did not resolve the existence of groups or subgenera within the genus. Phaeomyiidae was discussed in some detail and was reinserted into the Sciomyzidae as a subfamily from both the DNA and combined data set analyses. Notably, Chapman *et al*. (2012) discussed their results primarily in relation to sciomyzid habitats and feeding behaviour evolution, whereas Tóthová *et al*. (2012) discussed their results primarily in relation to taxonomy and phylogenetic relationships. Of the three publications including molecular data, the only Afrotropical species studied was *Ethiolimnia geniculata* (Loew, 1862) (Chapman *et al*. 2012). Nearctic and Palaearctic species of genera occurring in the Afrotropical Region included three species of *Sepedon* (Chapman *et al*. 2006, 2012) and two (different) species of *Sepedon*, two species of *Colobaea* and two species of *Pteromicra* Lioy (Tóthová *et al*. 2012).

Evenhuis (1994: 430) cited 13 species of fossil Sciomyzidae described in six genera from the Tertiary. Vala *et al*. (2012) listed the known species from the Oligocene, Eocene and Miocene. Poinar (2013) described a new genus with a new species from Dominican amber (between Upper Eocene to Lower Miocene Mamey Group). Some species from Baltic amber are awaiting description (M. von Tschirnhaus pers. comm. 2014).

Identification

Sciomyzids occur throughout the major zoogeographical regions, where they are variable in numbers of genera and species. No single species is cosmopolitan and various genera are absent from some regions. A few species are common to two or three adjacent regions. *Pherbellia*, with 97 species globally, is the most speciose genus and *Sepedon*, with 79 species. While most species are in the Oriental and Palaearctic Regions, only two species are cited in the Neotropical Region.

The described Afrotropical species (in one genus) are all in the subfamily Salticellinae and in the subfamily Sciomyzinae (four genera of Sciomyzini and seven genera of Tetanocerini) as detailed below. Identification keys to genera were provided by Knutson (1968), Knutson & Vala (2011: 300), Miller (1995) and Verbeke (1950, 1961) and for West Africa by Knutson *at al*. (2018). Identification keys to species were presented by Verbeke (1950) for *Pherbellia* (*Graphomyzina*), *Sepedoninus*, *Sepedon* and *Sepedonella* and Verbeke (1962*a*, *b*) for *Ethiolimnia*. Sciomyzidae are either direct-pinned or micro-pinned in the field for later double-mounting (see Chapter 2).

Figs 78.70–72. Larval predation of Sciomyzidae: (70) third-instar larva of *Tetanocera ferruginea* Fallén, consuming Afrotropical *Bulinus* sp.; (71) same, consuming Afrotropical *Biomphalaria glabrata* Say; (72) third-instar larva of *Sepedonella nana* Verbeke, inside tube of freshwater oligochaete, *Aulophorus furcatus* (Müller).

Abbreviations: 3 in lar – third-instar larva; air b – air bubbles; ol tub – oligochaete tube.

Only 65 described valid sciomyzid species have been reported from the Afrotropical Region. The first, *Sepedon* (*P.*) *senegalensis* Macquart, 1835, was described by Macquart (1844: 177) and most others in the series of publications by Verbeke (1950, 1956, 1961, 1962a, *b*, 1963), who described 42 species, *i.e.*, 66% of the known Afrotropical species. Additional species were described by Barraclough (1985), Knutson (1968), Knutson *et al.* (2018), Steyskal & Verbeke (1956) and Vala *et al.* (1994). In addition, one species was synonymised by Knutson (1980: 600) and two by Miller (1995), including Barraclough's species described in 1985. Recently, Knutson *et al.* (2018) described three new species and proposed (or suspected) three new synonymies.

Species are ascribed to 12 genera, of which four were erected by Verbeke (1950) and one by Knutson (1968). Four genera, *Ethiolimnia*, *Sepedonella*, *Tetanoptera* Verbeke and *Verbekaria*, appear to be endemic to the Afrotropical Region. The eight other genera included in the below generic identification key are also found elsewhere, in one or more zoogeographical regions. Knutson (1980: 597) provided the first synonymical catalogue of Afrotropical species. Vala *et al.* (2012, 2013) listed the current world species with their zoogeographical distribution, the institutions where the name-bearing type specimens are deposited and listed the world species in a tabular format, showing additional information, such as behavioural group, phenological group, *etc*. A number of undescribed species are in diverse museums and personal collections of entomologists, especially that of R.D. Miller.

Many of the described species are limited to the type collections, especially for species of monotypic genera. Many species are known only from the national parks of Democratic Republic of the Congo, as cited in Verbeke's publications, which contain useful ecological information and description of biotopes. Distribution maps have been provided for *Salticella stuckenbergi* (Kirk-Spriggs & McGregor 2009; Knutson *et al.* 1967), *Sepedon* (*Parasepedon*) *ruficeps* and *S.* (*P.*) *scapularis* (Knutson *et al.* 1967). Distributions have been published for the 14 species collected in 48 localities in Benin: *Sepedon* (*Mesosepedon*) *knutsoni*, *S.* (*P.*) *lippensi* Verbeke, 1950, *S.* (*P.*) *maculifemur* Verbeke, 1950, *S.* (*Sepedomyia*) *nasuta* Verbeke, 1950, *S.* (*P.*) *neavei*, *S.* (*P.*) *ornatifrons*, *S.* (*P.*) *ruficeps*, *S.* (*P.*) *straeleni* Verbeke, 1956, *S.* (*P.*) *testacea*, *S.* (*P.*) *trichrooscelis*, *S.* (*P.*) *umbrosa*, *Sepedonella nana*, *Sepedoninus curvisetis* and *Sepedoninus planifrons* Verbeke, 1950 by Agboho *et al.* (2017) and Gbedjissi (2003). Knutson *et al.* (2018) outlined the distribution of 20 Sciomyzidae species recorded from West Africa.

As Oman and United Arab Emirates are considered part of the Afrotropical Region, the six species that occur in the Southern Arabian Peninsula are here listed. These include Oriental, Palaearctic and traditional Afrotropical elements: Steyskal & Verbeke (1956) recorded *Sepedon* (*P.*) *ruficeps* (as *S.* (*P.*) *adamsi* Steyskal) and *S.* (*P.*) *edwardsi* Steyskal, 1956 from Yemen; Knutson & Orth (1984) recorded *S.* (*Sepedon*) *aenescens* from Oman; and Deeming & Dawah (2014) recorded *S.* (*P.*) *ruficeps* from Saudi Arabia, *S.* (*S.*) *aenescens* from Oman, *S.* (*P.*) *maculifemur* from Yemen, *Ditaeniella grisescens* from Saudi Arabia and *Pherbellia* (*Graphomyzina*) *kivuana* Verbeke, 1950 from Saudi Arabia and Yemen. *Sepedon* (*S.*) *aenescens* is widespread in the Oriental Region and the far eastern Palaearctic Region in the north to the northern Amur area and the Kuril Is. and in far eastern Russia and Hokkaido Is., Japan. *Ditaeniella grisescens* is very widely distributed in the Palaearctic, ranging from Iceland to far eastern Russia and south to Egypt, Israel, Iran, Mongolia and northern China. The other species are widespread elsewhere in the Afrotropical Region. It is likely that the genus *Sepedomerus*, known from Central and West Africa and Borneo and Sulawesi, will be found in this extended part of the Afrotropical Region.

Knutson & Vala (2011: 362) noted: 1) the absence of dispersal of sciomyzid faunas between the Afrotropical and the Nearctic Regions, between the Afrotropical and the Neotropical Regions and among the south temperate areas of Africa, South America, Australia and New Zealand; 2) proliferation of three genera of the *Sepedon* lineage in the Afrotropical Region; and 3) presence of two species of the Holarctic genus *Pteromicra* in Nigeria and Tanzania, which may indicate dispersal from the Palaearctic across North Africa during pluvial periods. Knutson *et al.* (2018) discussed the distribution, zoogeographical relationships and possible dispersal routes of some Afrotropical Sciomyzidae, namely: *Colobaea*, *Ditaeniella* and *Sepedon*. Currently, the genus *Salticella* includes three species: the fossil *Prosalticella succini* Hennig, 1965, described from Baltic amber and two extant species, *Salticella fasciata* (Meigen, 1830), mainly occurring in the western Palaearctic Region and circum-Mediterranean area (but not yet recorded from Morocco) and *Salticella stuckenbergi*, known from only four localities in Lesotho and South Africa. The probable dispersion route of the genus, originally from the Holarctic Realm and dispersed to Africa, could be similar to that of *Schistostoma* Becker (Dolichopodidae), as reported by Kirk-Spriggs & McGregor (2009).

Key to genera of Afrotropical Sciomyzidae

1. Wing cell *cua* with triangular apical extension; veins R_{4+5} and M_1 strongly convergent at wing apex (Fig. 13) (SALTICELLINAE) . . . . . .*Salticella* Robineau-Desvoidy
– Wing cell *cua* without triangular apical extension; veins R_{4+5} and M_1 parallel or slightly convergent at wing apex (SCIOMYZINAE) (*e.g.*, Figs 14, 15). 2
2. Thorax with ventral part of proepisternum with 1 usually strong seta, sometimes small or weak; male terminalia with 2 pairs (anterior and posterior) of well-developed surstyli, but anterior surstylus reduced in *Ditaeniella* (SCIOMYZINI) 3
– Thorax with ventral part of proepisternum without strong seta, only fine setulae present; male terminalia with 1 pair of well-developed posterior surstyli, anterior surstylus sometimes appearing as vestigial (distinct in *Ethiolimnia*) (TETANOCERINI) 6

3. Wing vein *CuA+CuP* not reaching posterior margin of wing (Fig. 14); antennal arista with dorsobasal microtrichia black, seta-like, much longer than other aristal microtrichia (Fig. 3); frons mostly pruinose; body mostly black and yellowish; length: 2.0–4.0 mm; fore coxa usually with 5 setae . . . . . *Colobaea* Zetterstedt

– Wing vein *CuA+CuP* reaching posterior margin of wing at least as a fold (e.g., Fig. 15); antennal arista without longer dorsobasal microtrichia (e.g., Fig. 4); frons mainly shiny black or pruinose; body not shiny black; length: 2.5–4.0 mm; fore coxa with maximum of 3 setae 4

4. Wing vein *CuA+CuP* reaching margin of wing as a fold (Fig. 15); head with gena narrow (Fig. 3); frons entirely shiny; shiny black species . . . . . *Pteromicra* Lioy

– Wing vein *CuA+CuP* distinctly reaching margin of wing as sclerotised vein; head with gena broad (e.g., Fig. 4); frons mostly pruinose, never entirely shiny; yellowish, greyish or brownish species, never shiny black 5

5. Head with 1 fronto-orbital seta (posterior) (Fig. 4); thorax with 2 anepimeral setae; hind coxa with inner posterodorsal margin with fine setae; wing membrane not patterned (Fig. 16); male terminalia with strong spines on postgonite; anterior surstylus reduced to small, setose lobe. . . . . *Ditaeniella* Sack

– Head with 2 fronto-orbital setae (anterior and posterior); thorax with 1 anepimeral seta; hind coxa with inner posterodorsal margin bare; wing membrane strongly patterned with numerous large, white maculae (Fig. 17); male terminalia without spines on postgonite; anterior surstylus well-developed . . . . . *Pherbellia* Robineau-Desvoidy

6. Scutellum with 2 pairs of marginal setae (basal and apical) (e.g., Fig. 10) 7

– Scutellum with 1 pair of marginal setae (apical) 9

7. Head with 2 fronto-orbital setae (anterior and posterior) (Fig. 2); wing membrane with brown costal border (Fig. 18); crossvein *dm–m* S-shaped, ending with small brown macula; a similar macula (sometimes 2) before and after this crossvein on vein M_1 (Fig. 18); male abdominal sternite 4 with pair of cylindrical processes . . . . . *Hydromya* Robineau-Desvoidy

– Head with 1 fronto-orbital seta (posterior) (as in Fig. 4); wing membrane variously patterned with maculae, fasciae, or reticulations (e.g., Figs 19–21); crossvein *dm–m* usually straight (S-shaped in some *Ethiolimnia*, Fig. 19) (e.g., Figs 20, 21); male abdominal sternite 4 without pair of cylindrical processes. . . . 8

8. Wing membrane either with dense, strongly reticulate pattern (Fig. 20) or brownish with several large, confluent transparent areas, mainly around mid-longitudinal axis (Fig. 19) . . . . . *Ethiolimnia* Verbeke

– Wing membrane brownish, with several large, rounded, transparent maculae (Fig. 21). . . . . *Verbekaria* Knutson

9. Head with ptilinal fissure; lunule distinct, broadly exposed (as in Fig. 2); frons entirely pruinose; ocellar setae weak; thorax with 2 notopleural setae; 1 postsutural supra-alar seta; wing membrane uniformly pale yellowish . . . . . *Tetanoptera* Verbeke

– Head without ptilinal fissure; lunule indistinct, not exposed; frons mostly shiny; ocellar setae weak or absent; thorax with 1 or 2 notopleural setae; 0–1 postsutural supra-alar seta; wing membrane greyish, usually apical portion infuscate (e.g., Figs 23–26) 10

10. Head without postocellar setae; very small species (body length: 3.5–5.8 mm); wing as in Fig. 23; male terminalia with posterior surstylus thin, elongate and stylus-shaped (Fig. 30), except quadrate in *S. castanea* Knutson & Deeming, 2018 (Fig. 31). . . . . *Sepedonella* Verbeke

– Head with postocellar setae; mostly larger species (body length: 5.0–9.0 mm); wing as in Figs 24–26; male terminalia with posterior surstylus not thin, elongate and stylus-shaped (e.g., Figs 35–37). 11

11. Head usually with 1 fronto-orbital seta (posterior), sometimes anterior fronto-orbital present, but weak, reclinate; lunular area not greatly inflated; thorax with transverse suture incomplete dorsally, without median portion (as in Figs 9, 10); wings as in Figs 25, 26 . . . . . *Sepedon* Latreille *sensu lato* 12

– Head with 2 fronto-orbital setae (anterior proclinate, posterior reclinate), both sometimes greatly reduced; lunular area very large, inflated; thorax with transverse suture complete dorsally (as in Fig. 11); wing as in Fig. 24. . . . . *Sepedoninus* Verbeke

12. Antennal scape longer than wide, at least ⅓ length of pedicel (Fig. 7); head with face perpendicular or strongly oblique; thorax with weak presutural supra-alar seta . . . . . *Sepedon* (*Sepedomyia* Verbeke)

– Antennal scape quadrate at most ⅓ length of pedicel (e.g., Fig. 6); head with face slightly oblique or slightly concave (e.g., Fig. 6); thorax with presutural supra-alar seta strong or weak, sometimes absent 13

13. Thorax without anterior notopleural seta; 1 strong presutural supra-alar seta; wing membrane mostly light greyish, or apex darkened; male terminalia with phallus without spiral filament; usually without cochleate vesicle . . . . . *Sepedon* (*Mesosepedon* Verbeke)

– Thorax sometimes with anterior notopleural seta; at most 1 weak presutural supra-alar seta, or absent; wing membrane without pattern or frequently apex darkened (Figs 25, 26); male terminalia with phallus usually with spiral filaments (Figs 38–41); often with cochleate vesicle (Figs 38, 42) . . . . . *Sepedon* (*Parasepedon* Verbeke)

Synopsis of the fauna

***Colobaea* Zetterstedt** (Sciomyzinae: Sciomyzini)**.** A genus of 15 described species occurring in the Afrotropical (1 species), Nearctic (3), Oriental (1) and Palaearctic (11, including *C. deemingi* Knutson & Bratt, 2020) Regions. The single Afrotropical species, *C. occidentalis* Knutson & Deeming, 2018, was described from Ethiopia, Niger and Nigeria (Knutson *et al*. 2018). In addition, an undescribed species is known from Gambia (R.D. Miller, unpubl.). *Colobaea* are very small species (body length: 2.0–3.5 mm), with the frons matt. The male terminalia has the anterior surstylus short with hair-like setae and the posterior surstylus of most species has short, peg-like processes (e.g., Knutson *et al*. 2018, fig. 3; Vala 1989, figs 21c, 22j, 22c). Habitats include open, wet ground to low herbaceous freshwater habitats. Bratt *et al.* (2020) published extensively on the biology and immature stages of one Nearctic and three Palaearctic species.

***Ditaeniella* Sack** (Sciomyzinae: Sciomyzini)**.** A genus of four described species occurring in the Afrotropical (1 species), Nearctic (2), Neotropical (1), Oriental (1) and Palaearctic (1) Regions. The single Palaearctic species, *D. grisescens*, also occurs in the Oriental Region (Rozkošný 1987; Vala 1989) and was recently recorded from Korea (Yeongjin & Sang 2019) and Japan (Sueyoshi 2001). *Ditaeniella grisescens* has been recorded from Egypt in North Africa and more recently from Saudi Arabia in the Arabian Peninsula (Deeming & Dawah 2014) and is expected to occur in the north-east of the Afrotropical Region. The genus was first mentioned as occurring in the Afrotropics by Miller (1991, 1995, Fig. 3), based on an undescribed species (close to *D. grisescens*), which occurs in Botswana, Namibia and South Africa. *Ditaeniella* are rather small species (body length: 3.0–4.5 mm), with the mid-frontal vitta elongated, with a tapered apex reaching the anterior margin of the frons and the frons bearing only one pair of fronto-orbital setae. The male terminalia have the anterior and posterior surstylus strongly reduced, and the postgonite bears prominent, strong spines (e.g., Vala 1989, figs 24a, 24c). Laboratory-reared first-instar larvae, bred from females of a *Ditaeniella* sp. collected from the Eastern Cape, South Africa, where only the freshwater snail *Bulinus tropicus* occurs, fed on various species of dead and dying aquatic snails in the laboratory, while second- and third-instar larvae were active predators of *Bulinus* species (Miller 1991, 1995). Habitats include mainly open ground wetland near permanent pools or various humid grassy and inundated areas. The biology and immature stages otherwise remain unknown and no identification key to Afrotropical species is currently available.

***Ethiolimnia* Verbeke** (Sciomyzinae: Tetanocerini)**.** An endemic Afrotropical genus of seven described species (Vala *et al*. 2012: 101). Knutson *et al.* (2018, table 1) indicated an additional four undescribed species in the region. One species, *E. zumpti* Verbeke, 1956, appears to be widespread, occurring in Cameroon, Ethiopia, Kenya and South Africa. The remaining species are known from Democratic Republic of Congo, Kenya, Namibia, Rwanda and South Africa. Knutson (1980: 598) placed *Limnia capensis* Schiner, 1868 in new combination with *Ethiolimnia*, but Miller (1995) later synonymised this species under *E. geniculata*. *Ethiolimnia* species are large (body length: 3.0–6.0 mm) and are distinguished by the brownish wing membrane with numerous large, clear maculae or more diffuse patterns (Figs 19, 20). These characters are similar to the two distinctive wing patterns of the Neotropical genus *Protodictya* Malloch, which may indicate one of the few relationships between Afrotropical and Neotropical Sciomyzidae. Verbeke (1950) noted that the genus was near *Limnia* Robineau-Desvoidy. The biology and immature stages remain unknown, but a small number of unidentified puparia were found within empty shells of the invasive White garden snail, *Theba pisana* (Müller) (Helicidae) among succulent dune plants on the Western Cape coast, South Africa, where *Ethiolimnia geniculata* was the dominant species (Miller 1995). Although no adults emerged from the numerous snail shells collected, the puparia exhibited characteristics similar to those of sciomyzid puparia but cannot be reported with certitude to be the aforementioned species. An identification keys to the seven described Afrotropical species was provided by Verbeke (1962*a*, *b*).

***Hydromya* Robineau-Desvoidy** (Sciomyzinae: Tetanocerini)**.** A monotypic genus, with the single described Palaearctic species, *H. dorsalis* (F., 1775), also recorded from the Oriental Region, in southern Egypt (Knutson & Berg 1963) and in Ethiopia in the Afrotropical Region (Miller 1995). This species, together with *Colobaea punctata* (Lundbeck, 1923), also cited in the Oriental Region and *Sepedon* (*Parasepedon*) *hispanica*, are the Palaearctic species extending into the Afrotropics. Li *et al*. (2019) first reported *H. dorsalis* from China. It is unique among Sciomyzidae in having two elongate, cylindrical processes on male abdominal sternite 4 (Vala 1989, fig. 82e). Larvae kill and consume diverse freshwater pulmonate snails and also feed in egg masses of the freshwater snails of the genus *Lymnaea* L. (Lymnaeidae) (Knutson & Berg 1963). Habitats include various freshwater environments.

***Pherbellia* Robineau-Desvoidy** (Sciomyzinae: Sciomyzini)**.** A large genus of 97 described species, occurring in all zoogeographical regions, except Antarctica. Species of the genus are small- to medium-sized (body length: 2.2–7.5 mm) and relatively similar to *Ditaeniella*, but differ by the presence of two pairs of fronto-orbital setae and the mid-frontal vitta varying in length. Currently, three Afrotropical species (nine globally) are included in the subgenus *P.* (*Graphomyzina* Macquart), mainly characterised by the absence of a mid-frontal vitta and presence of maculate wings (Fig. 17). *Pherbellia* (*G.*) *cingulata* (Verbeke, 1950) was described from Democratic Republic of Congo, *P.* (*G.*) *costata* (Verbeke, 1950) has been recorded

from Nigeria, Rwanda, South Africa, Zambia and Zimbabwe and *P.* (*G.*) *kivuana* (Verbeke, 1950) has been recorded from Democratic Republic of Congo, Nigeria and Rwanda (Knutson 1980: 598). Deeming & Dawah (2014) also reported *P.* (*G.*) *kivuana* from Yemen in the Afrotropics and Saudi Arabia in the Palaearctic. An undescribed species from Tanzania was cited by Miller (1995). The life cycles of many extralimital species have been published, mainly by Bratt *et al.* (1969). Habitats include various terrestrial to freshwater areas. The three described Afrotropical species can be identified by reference to Verbeke (1950), bearing in mind that at least one undescribed species is known.

***Pteromicra* Lioy** (Sciomyzinae: Sciomyzini)**.** A genus of 19 described species occurring in the Afrotropical, Nearctic, Oriental and Palaearctic Regions. Two species occur in the Afrotropics, the recently described *P. zariae* (Knutson & Deeming, 2018) from Nigeria in West Africa (Knutson *et al.* 2018) and one undescribed species from Tanzania, which represents the first record of the genus in East Africa. *Pteromicra* are small-sized (body length: 2.0–4.0 mm), with the frons entirely shiny and the hypandrium of the male terminalia bearing a pair of pubescent lobes (in posteroventral view) (Knutson *et al.* 2018, fig. 5). Habitats include the margins of freshwater bodies and grassland.

***Salticella* Robineau-Desvoidy** (Salticellinae)**.** A genus of two described species occurring in the Afrotropical and Palaearctic Regions. One species, *S. stuckenbergi*, occurs in the Afrotropics, in Lesotho and South Africa, and is the largest known sciomyzid (body length: 14 mm). Among the Sciomyzidae, this genus is considered the most plesiomorphic branch form, along with the subfamily Phaeomyiinae. The genus is mainly characterised by the triangular shape of the anterior cubital wing cell (*cua*), extending along vein *CuA+CuP* (Fig. 13); convergence of veins R_{4+5} and M_1 at the wing apex (Fig. 13); and presence of four spermathecae in the female. The larvae of *S. stuckenbergi* were observed apparently scavenging on decomposing terrestrial pumonate snails of the genus *Archachatinina* Albers (Achatinidae), but possibly also feed on other terrestrial snails (Miller 1995). This is similar to observations made by Knutson *et al.* (1970), who found that *S. fasciata* was able to develop in a parasitoid, predacious or saprophagous manner. As first reported by Knutson *et al.* (1970), the female lays 1–6 eggs in the umbilici of *Helicella virgata* (Müller). Examination of 100 living *Theba pisana* collected in the south of France revealed that 83 had eggs of *Salticella* (Vala 1989: 50). In cases where snails had several eggs present, only a single larva reached the puparial stage, indicating intense intraspecific competition between larvae. Vala (1989: 51) found larvae to be parasitoids/saprophagous, liquefying the tissues of living snails of the genus *Helicella* Férussac (Hygromiidae) and *Theba pisana* prior to ingestion. Coupland *et al.* (1994), however, noted that females laid eggs only on moribund *T. pisana* and *Cernuella virgata* (Da Costa) (Geomitridae) snails in nature and considered larvae to be strictly saprophagous (see further discussion in Knutson & Vala 2011: 2, 85). The immature stages of the Afrotropical species have not been described. Habitats include various dry areas, such as herbaceous grasslands, forest margins, dormant vineyards and coastal dunes.

***Sepedon* Latreille** (Sciomyzinae: Tetanocerini)**.** A genus of 79 described species, occurring in all zoogeographical regions, except Antarctica. *Sepedon* is the largest genus of Sciomyzidae in the Afrotropics, with 64% of the described species in the world. The genus is taxonomically distinctive, based on morphological characters of adults, particularly the male terminalia. The Afrotropical species are divided into four subgenera. Most species are included in the subgenus *S.* (*Parasepedon*) (34 species) and are characterised by the presence of spiral filaments on the distiphallus (Figs 38–41) and a unique, complex sperm pump, first described by Verbeke (1961). This is the cochleate vesicle, which Steyskal & Knutson (1975) described and figured in detail (Figs 38, 42). This feature is also present in some *Sepedon* species occurring in the Australasian and Oriental Regions. The subgenus *S.* (*Mesosepedon*) (7 species) is characterised by the absence of this structure. Verbeke (1950) proposed the subfamily Sepedoninae, including *Sepedon* (divided into nine species-groups) and his three new Afrotropical genera *Sepedomyia*, *Sepedoninus* and *Sepedonella*. This subfamily has not been generally accepted in the sciomyzid literature, but should be reconsidered with addition of the allied genera cited above and with consideration of additional characters of the adult and immature stages, biology and DNA analyses. Earlier, Steyskal (1973: 145) considered the genus *Sepedomyia* as a subgenus of *Sepedon*, on the criterion "… 1st antennal segment somewhat elongate." Knutson (1980: 599) applied this modified rank in his Afrotropical Sciomyzidae catalogue. Barraclough (1985: 489) considered that the subgeneric status appears to be valid "… because *Sepedomyia*, [2 species], are clearly distinguished from other *Sepedon* species by the longer scape, presence of a humeral seta [more or less reduced] and a [very] distinct hypopygial structure..." This author noted (p. 489), "... the Afrotropical *Sepedon* fauna is rather poorly known, so a final decision on the status of the subgenera should be taken after a comprehensive revision of the genus in the region…" In a subsequent analysis, Knutson & Orth (2001), placed Verbeke's subgenera of *Sepedon* in nine new groups, different from the nine groups established by Verbeke (1950, 1961), including *Mesosepedon* + *Parasepedon* + *Sepedomyia* and indicated the known life cycles and immature stages. The Afrotropical species are included in their species-groups 6 (*Trichrooscelis* = subgenus *S.* (*Parasepedon*)), 7 (*Dispersa* = subgenus *S.* (*Mesosepedon*)) and 9 (*Nasuta* = subgenus *S.* (*Sepedomyia*)). Verbeke's classification of *Sepedon* into subgenera and nine species-groups is discussed in Knutson *et al.* (2018). The taxonomic classification and phylogenetic relationships of *Sepedon* and related genera remain an open question. As noted above, in their phylogenetic analyses, Barker *et al.* (2004: 172) and Marinoni & Mathis (2000) recovered this assemblage at the terminus of their trees. Chapman *et al.* (2012), however, from their phylogenetic analyses of 62 species in 20 genera of Tetanocerini based on DNA characters, recovered *Sepedon* near the base of their tree, between *Psacadina* Enderlein + *Anticheta* Haliday and the remainder of the Tetanocerini. The biology and immature stages of many species have been extensively studied and described; see Knutson & Orth (2001) and Vala *et al.* (2012) for tabulations of publications. Most *Sepedon* species prey upon freshwater pulmonate snails. Neff & Berg (1966) provided the essentials on the biology of many species of *Sepedon*. Biology and morphology of the immature stages and life cycles are known partially or completely for 11 Afrotropical *Sepedon* species: *S.* (*P.*) *hispanica* (Knutson *et al.* 1967), plus details on the third-instar larva and puparium of *S.* (*P.*) *scapularis* and *S.* (*P.*) *ruficeps*;

S. (*P.*) *neavei*, *S.* (*P.*) *testacea* (Barraclough 1983); *S.* (*P.*) *trichrooscelis* (Vala *et al*. 1995) and Knutson (2008), additional data on its parasitoid feeding behaviour; *S.* (*M.*) *knutsoni* (Vala *et al*. 2002) on the biology, Gbedjissi (2003) on the life cycle; *S.* (*P.*) *ruficeps* (Gbedjissi *et al*. 2003) on the biology, Gbedjissi & Vala (2014) on the life cycle; *S.* (*P.*) *ornatifrons* (Gbedjissi 2003); *S.* (*P.*) *umbrosa* (Gbedjissi 2003, on the biology and Gbedjissi *et al*. 2020, on the life cycle); and *S.* (*Sepedomyia*) *nasuta* (Agboho *et al*. 2019) on the biology and life cycles. Most species occur in or near freshwater habitats, temporary herbaceous pools and in seasonally flooded areas, but a few are terrestrial or semi-terrestrial. Afrotropical species can be identified by reference to the identification keys provided by Verbeke (1950), supplemented by the identification key provided by Knutson *et al*. (2018) for West Africa.

***Sepedonella* Verbeke** (Sciomyzinae: Tetanocerini)**.** An endemic genus of five described species: *S. bredoi* Verbeke, 1950, *S. straeleni* Verbeke, 1956 and *S. wittei* Verbeke, 1950, all exclusively from Democratic Republic of Congo; the more widespread *S. nana*, from Chad, Democratic Republic of Congo, Ethiopia, Kenya, Lesotho, Nigeria, Senegal and South Africa; and a fifth species, *S. castanea*, recently described from Cameroon and Nigeria (Knutson *et al*. 2018). The genus is easily distinguished from others by the small size (body length: 3.5–5.0 mm) and the slender, elongated body. General characters are as described for *Sepedon* above, but the postocellar setae are absent. The male surstylus is of a specific shape, being thin, stylus-like and elongated (Fig. 30) and there is no phallic filament or separate apodeme. The exception is *S. castanea* (Fig. 31). Knutson *et al*. (2018: 93) wrote "… surstylus unlike other species of the genus, not elongate, apically quadrately dilated in profile (fig. 27)." Only the life cycle of the widespread *S. nana* is known. Larvae feed on small freshwater oligochaetes (Vala & Gbedjissi 2011; Vala *et al*. 2000*a*, *b*). Species occur mainly in permanent freshwater habitats. Afrotropical species can be identified by reference to the identification keys provided by Verbeke (1950), supplemented by the key provided by Knutson *et al*. (2018) for West Africa.

***Sepedoninus* Verbeke** (Sciomyzinae: Tetanocerini)**.** Initially, this genus was established by Verbeke (1950) with three described species: *S. curvisetis*, from Cameroon, Democratic Republic of Congo, Kenya and Nigeria; *S. planifrons*, from Democratic Republic of Congo and Uganda; and *S. straeleni* Verbeke, 1950, subsequently synonymised with the second species by Knutson (1980: 600). These are mainly reddish yellow, relatively large (body length: 8.0–9.0 mm), narrow and elongated species. The fronto-orbital maculae are particularly large and rounded and the two fronto-orbital setae (anterior proclinate and posterior reclinate for *S. curvisetis*) are sometimes microscopic, reduced or absent. The antennae are longer than the head. The antennal pedicel is greatly elongated and slightly tapered, with elongate dorsal setae, curved or not. The thoracic transverse suture is remarkably deep and complete (Fig. 11). Abdominal segment 3 is greatly elongate. The phallic filament is not spiralled. Two undescribed species are known, one from Madagascar and one from Borneo in the Oriental Region (Vala 2018), indicating that the genus is not restricted to the Afrotropics, as previously thought. The egg and third-instar larva of *S. curvisetis* were described by Agboho *et al*. (2019). Species occur in permanent freshwater pools, lakes and temporary herbaceous ponds. Afrotropical species can be identified by reference to the identification keys provided by Verbeke (1950), supplemented by the identification key provided by Knutson *et al*. (2018) for West Africa.

***Tetanoptera* Verbeke** (Sciomyzinae: Tetanocerini)**.** An endemic monotypic genus, with the single described species, *T. leucodactyla* Verbeke, 1950, described from the unique female holotype from Democratic Republic of Congo. The male was later described from Democratic Republic of Congo by Knutson & Vala (1999). The hind femur is swollen in the male and simple in the female and the phallapodeme of the male terminalia is umbrella-shaped. Knutson & Vala (1999) compared the synapomorphic/plesiomorphic state of 25 characters amongst 12 genera and concluded that *Tetanoptera* appeared to be related to *Verbekaria* and the non-Afrotropical genus *Thecomyia*. The biology and immature stages remain unknown. The holotype was collected at Kivu, near the volcano Mikeno, at an elevation of 2,400 m (Verbeke 1950).

***Verbekaria* Knutson** (Sciomyzinae: Tetanocerini)**.** An endemic monotypic genus, with the single described species, *V. punctipennis* Knutson, 1968, described from two females collected in eastern Tanzania. The male was later described by Vala *et al*. (2000*c*) from a specimen collected close to the type locality. Generic characters are close to the *Sepedon*-group with the wing membrane brownish, iridescent and a faint pattern of large, round, hyaline irrorations (Fig. 21). The biology and immature stages remain unknown. The species occurs in montane rainforest.

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SEPSIDAE 79

(Sepsid Flies or Ant-like Scavenger Flies)

Andrey L. Ozerov

Fig. 79.1. Male of *Toxopoda* (*Platytoxopoda*) *bequaerti* (Curran) (Tanzania) (photograph © D. Gavryushin).

Diagnosis

Small- or medium-sized (body length: 2–12 mm) black, rarely grey, or yellow acalyptrate flies, superficially resembling winged ants (Figs 1–4).

Head (Figs 5–7) roundish or long-oval; eyes large, bare, dichoptic in both sexes; face usually with well-developed facial carina and antennal grooves, very narrow in *Afrosepsis* Ozerov (Fig. 7); antenna ventrally directed; antennal postpedicel long-oval (Fig. 6); arista bare, with 3–4 long dorsal branches in *Idiosepsis* Ozerov only (Fig. 6); palpus very short, slender; 0–1 fronto-orbital seta, 1 ocellar seta, 0–1 divergent postocellar seta, 0–1 inner vertical seta, 0–1 outer vertical seta present; lateral occipital sclerite with several short setae, absent in *Paratoxopoda* Duda; 1–3 vibrissae present.

Thorax elongate or wide in some *Brachythoracosepsis* Ozerov; scutum moderately convex, with postpronotal lobes distinct; 0–1 postpronotal seta, 1–2 notopleural setae, 0–1 supra-alar seta, 0–2 postalar setae, 0 + (1–3) dorsocentral setae present; intra-alar setae and acrostichal setae absent; postmetacoxal bridge present (in *Adriapontia* Ozerov, *Brachythoracosepsis*, *Dicranosepsis* Duda, *Paratoxopoda* and *Toxopoda* Macquart) (Fig. 10), or absent (Fig. 9); lower margin of posterior spiracle with 1 or more setae (Fig. 8). Scutellum short, slightly convex dorsally, but flattened in *Saltella* Robineau-Desvoidy. Wing (Figs 15–23) well-developed, usually hyaline, or with infuscate area near tip (*Nemopoda* Robineau-Desvoidy and some *Brachythoracosepsis*); some *Sepsis* Fallén with dark oval macula at tip of vein R_{2+3} (Fig. 17); costal vein (*C*) without breaks; subcostal vein (*Sc*) complete (Fig. 15); *bm* and *br* cells distinct, but fused in *Australosepsis* Malloch (Fig. 18) and *Saltella* (Fig.

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2021. Manual of Afrotropical Diptera. Volume 3. Brachycera—Cyclorrhapha, excluding Calyptratae. *Suricata* 8. South African National Biodiversity Institute, Pretoria; pp. 1847–1859.

15); anal lobe and alula well-developed to narrow in *Afrosepsis* (Fig. 20) and *Brachythoracosepsis* (Fig. 19); alula usually clothed in microtrichia, but entirely bare in certain *Australosepsis*, *Paratoxopoda* and *Xenosepsis* Malloch; upper calypter well-developed, with fringe of long setulae; lower calypter linear, margin usually bare, but with long setulae in *Idiosepsis* and *Paratoxopoda*. Legs rather long and slender; as a rule, Sepsidae demonstrate sexual dimorphism in structure of fore and hind legs; fore femur and fore tibia of males usually with spines, pegs, teeth, tubercles, protuberances or excisions (Figs 29–34) (assist males with clasping females at wing base during copulation); fore femur and fore tibia of females usually simple; male hind tibia in several genera with dorsal field-like scent organ "osmeterium" (function and effect on female behaviour unknown (Pont & Meier 2002)); both males and females of *Diploosmeteriosepsis* Ozerov with osmeterium on fore coxa (Fig. 11).

Abdomen slender, cylindrical, shiny to subshiny; male segment 1 + 2 often constricted, very strongly so in *Brachythoracosepsis* (Fig. 14), *Diploosmeteriosepsis* and *Leptomerosepsis* Duda; male tergite 6 absent, tergites 7 and 8 fused; male sternite 4 simple to highly modified (Figs 24–28), often used for specific identification; surstyli symmetrical (Figs 37–42), asymmetrical in *Idiosepsis* (Figs 35, 36) and some *Toxopoda* only, completely or incompletely fused to epandrium, simple or modified.

Adults Sepsidae are easily distinguished from other families of acalyptrate Schizophora by the presence of one or more setae on the lower margin of the posterior spiracle (Fig. 8).

Biology and immature stages

Adults and larvae are associated mostly with animal dung, excrement and mammalian carrion, but are sometimes also found on other decaying substrates, such as decomposing algae, fungi, plants and soil rich in decaying organic matter. Adults may also be encountered on flowers, decomposing fruits and oozing tree sap (e.g., Pont & Meier 2002).

Larvae of most sepsid species develop in the dung of hoofed mammals, being significant utilisers of cattle dung and similar substrates, in both anthropogenic landscapes and nature. The larvae of many species are capable of developing in more than one breeding medium, although cases of larvae developing in very diverse substrates, such as decaying plant material and mammalian carrion are rare. There are by contrast, a few cases in which some Palaearctic species are highly adapted to a single breeding medium, examples being: *Orygma luctuosum* Meigen, 1830 in brown algae, *Ortalischema* Frey and *Zuskamira inexpectata* Pont, 1987, in equine dung and some *Themira* Robineau-Desvoidy in waterfowl dung (Meier 1996; Pont & Meier 2002).

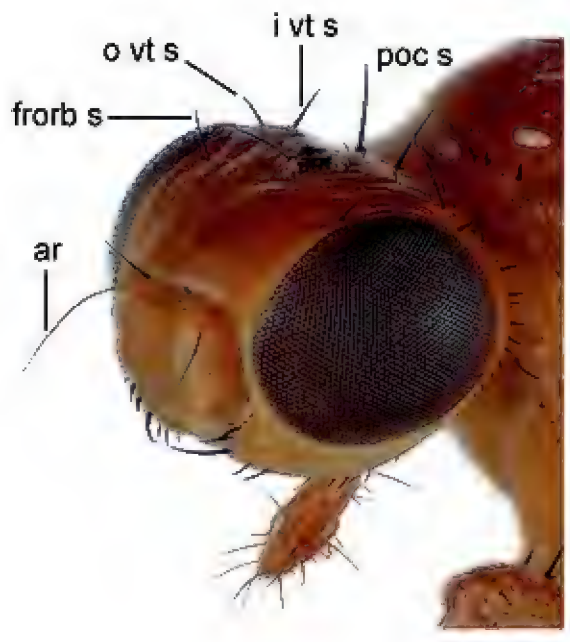
Adult flies can be choosey and will only settle on substrates of certain age and level of decay for breeding purposes; although females are less choosey when obtaining protein for oogenesis. As a rule, females avoid waterlogged substrates, dry substrates or those which may desiccate too rapidly. For this reason, females of Sepsidae do not normally oviposit on droppings of small antelopes, sheep, or on corpses of small Amphibia, Reptilia or Arthropoda.

Adult sepsids are agile fliers, but are disinclined to fly for long distances. As such, they do not disperse far from breeding areas. In open habitats they may be found on vegetation near the soil surface. Males of numerous species occupy and guard territories on the substrate or in the vegetation nearby to await incoming females.

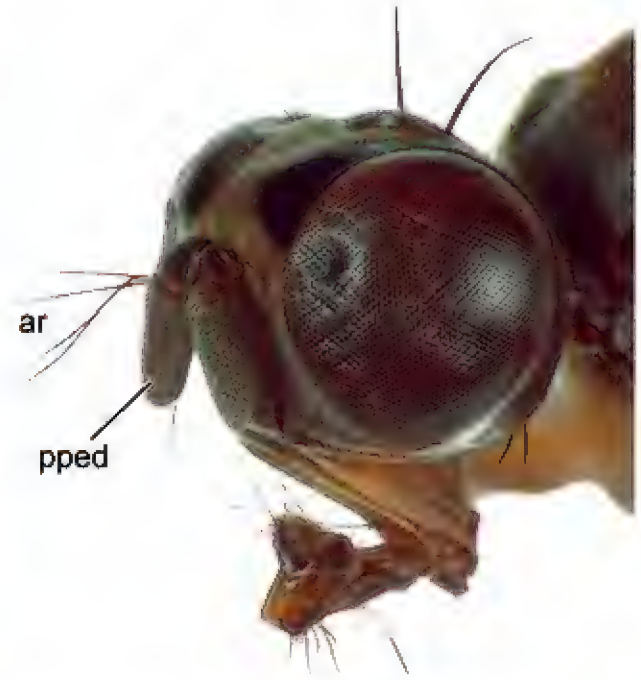
During mating, males of most species use their modified fore legs to clasp onto the female's wing base, but the morphological modifications of the fore legs are lost in some species that do not clasp (Ang *et al*. 2008; Puniamoorthy *et al*. 2008). Mating behaviour is very diverse and usually involves all pairs of legs as discussed and illustrated in Puniamoorthy *et al*. (2009). The significance of the morphology of the fore legs has been discussed by Allen & Simmons (1996), but the morphological diversity in male legs is (surprisingly) not matched by similar degrees of morphological diversity in female wings (Ingram *et al*. 2008).

Eggs of most sepsid species (including *Nemopoda*, *Paratoxopoda* and *Sepsis*) have respiratory filaments that are many times longer than the egg. The length of the filament is loosely correlated with the liquid consistency of the substrate into which

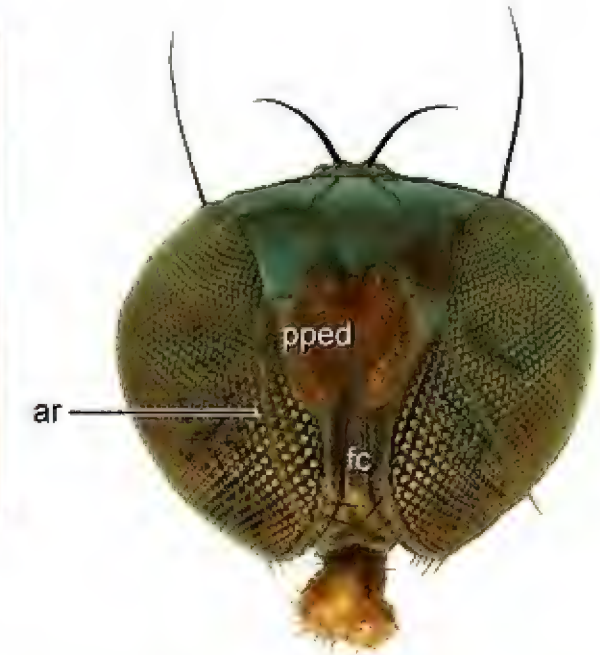
Figs 79.2–4. Photographs of living Afrotropical Sepsidae: (2) *Australosepsis niveipennis* (Becker) (Tanzania); (3) *Sepsis lateralis* Wiedemann (Tanzania); (4) *Adriapontia capensis* (Hennig) (South Africa). Figs 2, 3 (photographs © D. Gavryushin), Fig. 4 (photograph © S.A. Marshall).



5 *Saltella* ♂

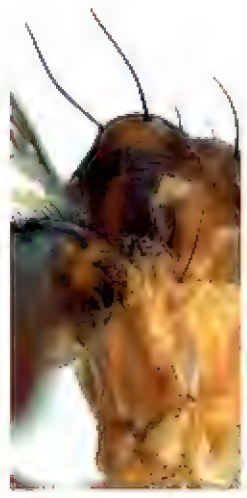


6 *Idiosepsis* ♂

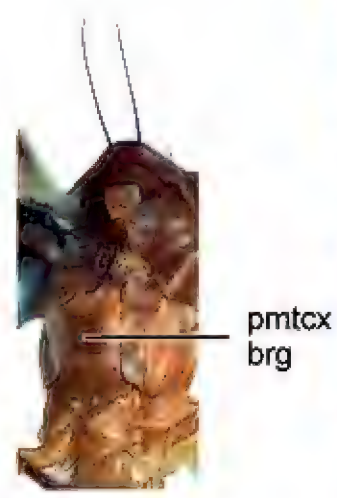


7 *Afrosepsis* ♂

8 *Sepsis* ♂



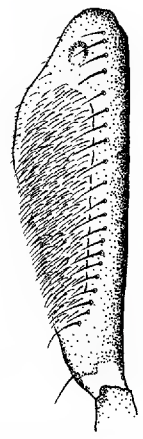
9 *Leptomerosepsis*



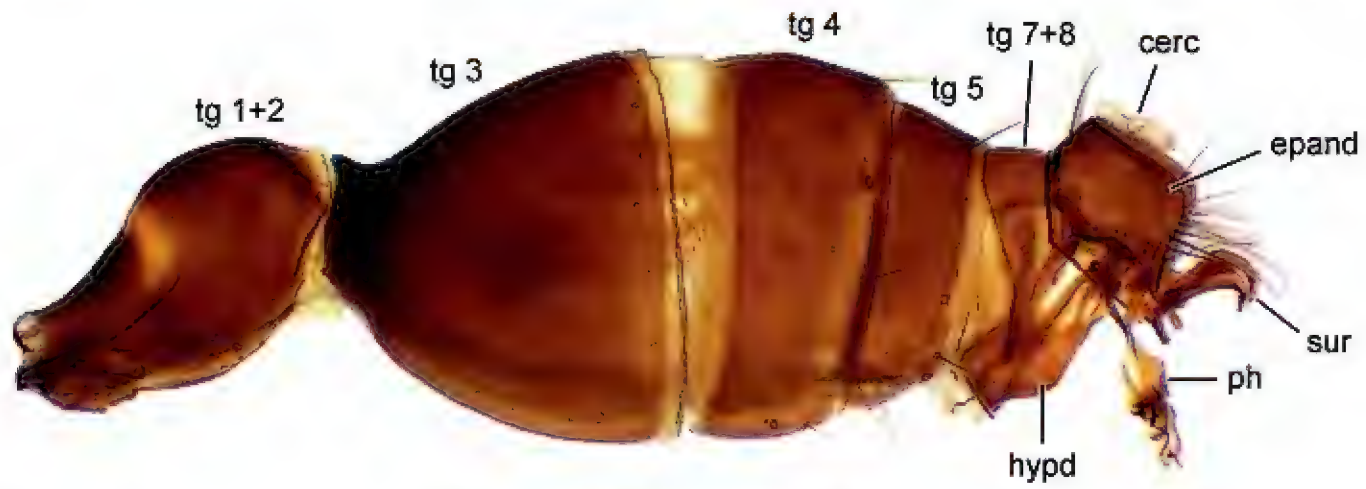
10 *Adriapontia*

12 *Sepsis* ♂

13 *Nemopoda* ♂



11 *Diploosmeteriosepsis* ♂



14 *Brachythoracosepsis* ♂

Figs 79.5–14. Male heads, thoraces, coxae and abdomen of Sepsidae: (5) head of *Saltella bezzii* (Duda), oblique view; (6) same, *Idiosepsis spangleri* Ozerov; (7) same, *Afrosepsis camerounica* Ozerov, frontal view; (8) posterior thoracic spiracle of *Sepsis lateralis* Wiedemann, lateral view; (9) posteroventral area of thorax posterior and dorsal to hind coxae of *Leptomerosepsis rubiginosa* Ozerov (postmetacoxal bridge absent); (10) same, *Adriapontia freidbergi* Ozerov (postmetacoxal bridge present); (11) osmeterium on fore coxa of *Diploosmeteriosepsis pilifemur* (Munari), lateral view; (12) mid coxa of *Sepsis lateralis* Wiedemann, anterolateral view; (13) same, *Nemopoda nitidula* (Fallén); (14) abdomen of *Brachythoracosepsis nodosa* (Walker), lateral view. Fig. 11 (Ozerov 1996, fig. 43).

Abbreviations: ar – arista; cerc – cercus; epand – epandrium; fc – face; frorb s – fronto-orbital seta; hypd – hypandrium; i vt s – inner vertical seta; o vt s – outer vertical seta; ph – phallus; pmtcx brg – postmetacoxal bridge; poc s – postocellar seta; pped – postpedicel; s – seta; sur – surstylus; tg – tergite.

sepsids tend to oviposit. Eggs are deposited within the substrate, with the long respiratory filament lying on the surface, allowing for ample gaseous exchange for the developing egg.

Females of the majority of species lay a single egg at a time and cases of 2–3 eggs being laid simultaneously are rare. *Saltella* females are, however, known to lay their eggs in a single batch (Ozerov 1986), as do some *Themira* (R. Meier, pers. comm. 2014). Such behaviour also occurs in some *Meroplius* Rondani, but rarely so (Ozerov 1991*b*).

Larvae (Figs 43–54) occur mostly within the substrate and generally only the posterior spiracles protrude; only occasionally are the anterior spiracles protruded. Larvae generally move slowly within the substrate, but if disturbed may move rapidly in a backwards and forwards motion. Sepsidae larvae are cylindrical, tapered anteriorly and thickened posteriorly and are usually white, or greyish white in colour. Having ceased feeding, mature larvae turn yellowish white prior to pupariation. Pupariation takes place either in the substrate, or in the soil nearby, or beneath the substrate. The duration of development from egg to adult varies in different species. Hafez (1939) reported 6–7 days for development of *Sepsis lateralis* Wiedemann, 1830, from egg to adult under field conditions, but the development of most species takes 14–18 days. The duration of larval development is dependent upon micro-climatic conditions and the state of the substrate. Temperature appears to be the most significant factor, with higher temperatures reducing development time (Modassir 1995).

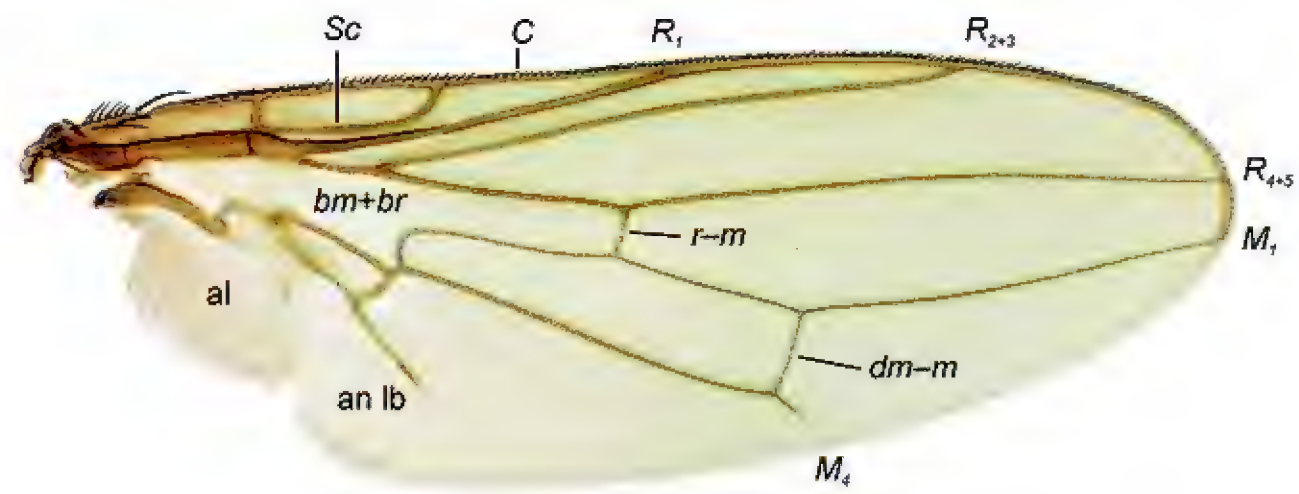
The following larvae of Afrotropical Sepsidae were described in detail by Meier (1996): *Nemopoda nitidula* (Fallén, 1820) (Figs 52–54), *Paratoxopoda amonane* (Vanschuytbroeck, 1961) (Figs 43–45), *Sepsis lateralis* (Figs 46–48) and *S. thoracica* (Robineau-Desvoidy, 1830) (Figs 49–51).

Economic importance

Sepsidae are an important family in the decomposition of cattle dung (Hammer 1941; Papp 1971) and other decaying substrates, including faeces. Nevertheless, they have a low potential as transmitters of pathogens, as they avoid human dwellings (Minder 1963). Some species of Sepsidae (*Saltella* and *Sepsis*), may be important for pollination (Bährmann 1993; Minder 1963).

Classification

Sepsidae is a small, morphologically uniform family of acalyptrate flies in the superfamily Sciomyzoidea. Sepsidae are monophyletic (Hennig 1949; Lei *et al*. 2013; Meier 1995*a*, *b*, 1996; Su *et al*. 2008), but phylogenetic relationships require more detailed analysis. The Neotropical family Ropalomeridae (non-Afrotropical), has long been regarded as the sister-group to the Sepsidae (McAlpine 1989: 1453; Pont &



Figs 79.15–17. Male wings of Sepsidae (dorsal views): (15) *Saltella bezzii* (Duda); (16) *Afronemopoda ealaensis* (Vanschuytbroeck); (17) *Sepsis kiribatensis* Vanschuytbroeck.

Abbreviations: al – alula; an lb – anal lobe; *bm* – basal medial cell; *bm+br* – basal medial cell + basal radial cell; *br* – basal radial cell; *C* – costal vein; *dm–m* – discal medial crossvein; M_1 – first branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Sc* – subcostal vein.

Meier 2002), but the support for this relationship is weak and based on two characters only: presence of a group of setae along the margin of the posterior spiracle; and fusion of the phallapodeme with the hypandrium in males. These characters may, however, have arisen convergently, given that Ropalomeridae and Sepsidae are not sister-groups according to the latest molecular analysis of Diptera relationships (Wiegmann *et al*. 2011).

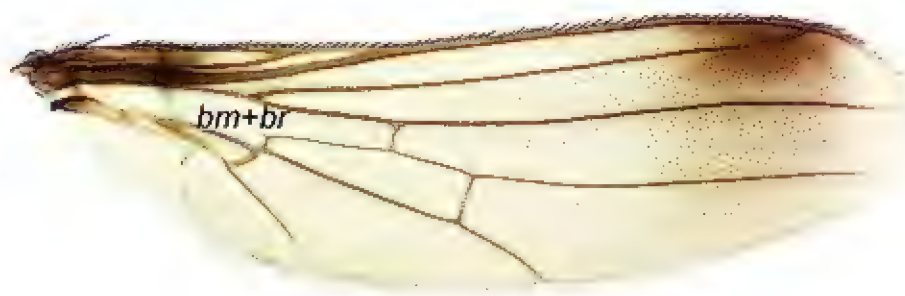
The phylogenetic relationships of the family require further study, although many relationships are now well understood, based on morphological and molecular data (Lei *et al*. 2013; Meier 1995*a*, *b*, 1996; Su *et al*. 2008). One puzzling finding is that the morphologically well-supported subfamilies Orygmatinae and Sepsinae (Ozerov 2003; Pont & Meier 2002), are not supported by molecular data, as *Orygma* Meigen and *Ortalischema* are sister-groups in all analyses involving molecular data. Phylogenetic relationships within the large subfamily Sepsinae that includes all the remaining genera and species are largely unresolved, other than the positions of certain genera as discussed in Lei *et al*. (2013).

Identification

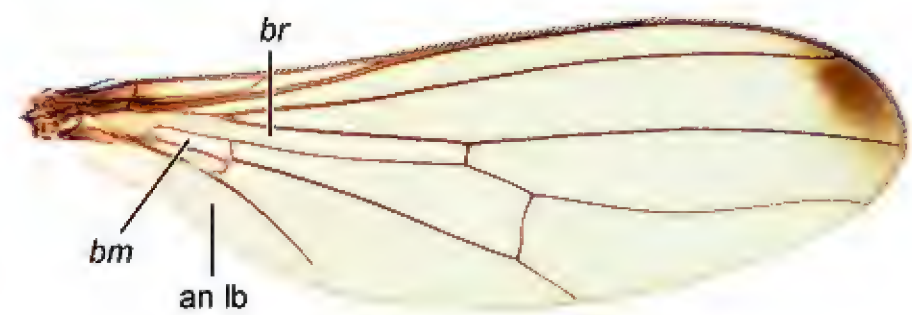
Duda's (1926*a*, *b*) monograph is fundamental to the study of Afrotropical Sepsidae. A modern identification key to Afrotropical genera was provided by Ozerov (2006) and the following genera have been revised: *Adriapontia* (Ozerov 2000*a*, 2014), *Afrosepsis* (Ozerov 1999*a*), *Meroplius* (Ozerov 1999*b*) and *Paratoxopoda* (Ozerov 1993). *Sepsis*, the largest genus of Afrotropical Sepsidae, is in need of revision.

Characters included in the following key should facilitate ready identification of adult Sepsidae to genera, but examination of male terminalia and the structure of the fore legs are required for specific identification. Unfortunately, the determination of females to species can be problematic and is sometimes impossible.

Sepsidae are best collected into individual glass vials (use of an aspirator tends to cause damage) and can either be micropinned in the field for later staging (see Chapter 2), or be preserved in alcohol.



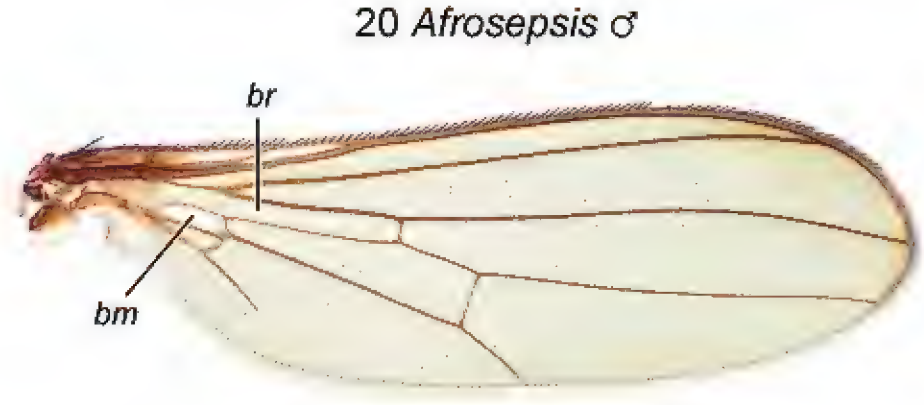
18 *Australosepsis* ♂



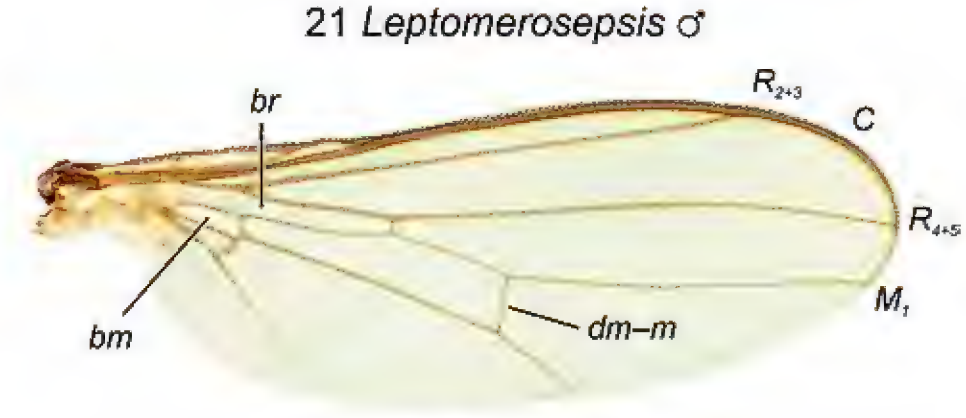
19 *Brachythoracosepsis* ♂

20 *Afrosepsis* ♂

21 *Leptomerosepsis* ♂



22 *Dicranosepsis* ♂



23 *Meroplius* ♂

Figs 79.18–23. Male wings of Sepsidae (dorsal views): (18) *Australosepsis niveipennis* (Becker); (19) *Brachythoracosepsis nodosa* (Walker); (20) *Afrosepsis quadrimaculata* Ozerov; (21) *Leptomerosepsis simplicicrus* (Duda); (22) *Dicranosepsis takoensis* (Vanschuytbroeck); (23) *Meroplius bispinifer* Ozerov.

Abbreviations: an lb – anal lobe; *bm* – basal medial cell; *bm+br* – basal medial cell + basal radial cell; *br* – basal radial cell; *C* – costal vein; *dm–m* – discal medial crossvein; M_1 – first branch of media; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius.

Key to genera of Afrotropical Sepsidae

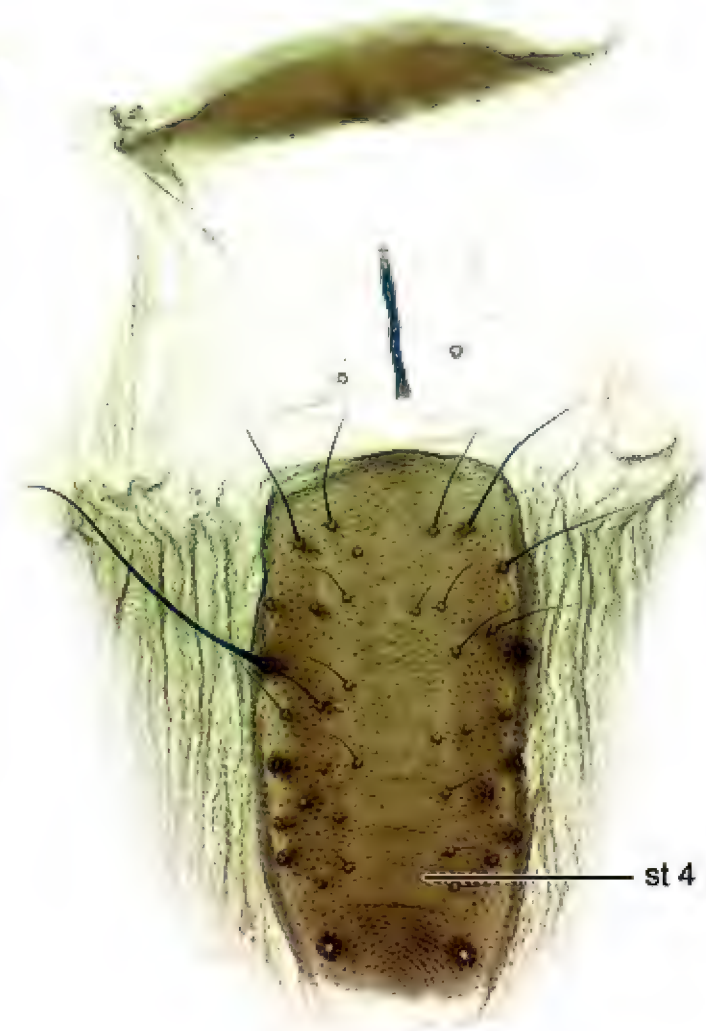
1. Thorax with postmetacoxal bridge; posteroventral area of thorax posterior and dorsal to hind coxae (between metepimera) sclerotised (e.g., Fig. 10) 2
– Thorax without postmetacoxal bridge; posteroventral area of thorax posterior and dorsal to hind coxae (between metepimera) membranous (e.g., Fig. 9) 6
2. Margin of lower calypter with setulae . . . . . *Paratoxopoda* Duda
– Margin of lower calypter without setulae 3
3. Head without inner vertical setae . . . . . *Toxopoda* Macquart
– Head with inner vertical setae 4
4. Thorax with mediotergite grey pruinose; male terminalia with surstyli not fused to epandrium . . . . . *Brachythoracosepsis* Ozerov
– Thorax with mediotergite at least shiny medially; male terminalia with surstyli fused to epandrium . . . 5
5. Thorax with katepisternum entirely greyish pruinose . . . . . *Adriapontia* Ozerov
– Thorax with katepisternum shiny in lower ½ . . . . . *Dicranosepsis* Duda
6. Wing with *bm* and *br* cells fused (e.g., Figs 15, 18) 7
– Wing with *bm* and *br* cells unfused (e.g., Figs 16, 17, 19–23) 8
7. Scutellum slightly convex, *ca* ½ as long as broad; head without fronto-orbital setae; wing with dark macula near tip (Fig. 18) . . . . . *Australosepsis* Malloch
– Scutellum strikingly flattened, approximately as long as broad; head with fronto-orbital setae (Fig. 5); wing without dark macula near tip (Fig. 15) . . . . . *Saltella* Robineau-Desvoidy
8. Antennal arista with 3–4 long branches dorsally (Fig. 6); head without orbital, occipital, outer and inner vertical setae; margin of lower calypter with setulae . . . . . *Idiosepsis* Ozerov
– Antennal arista bare (e.g., Figs 5, 7); head with at least outer and inner vertical setae; margin of lower calypter without setulae 9
9. Mid coxa with strong seta in dorsal ½ (e.g., Fig. 13) 10
– Mid coxa without strong seta in dorsal ½, bare or with vertical row of thin setulae (e.g., Fig. 12) 11
10. Scutum with 1 + 3 dorsocentral setae . . . . . *Afromeroplius* Ozerov
– Scutum with 1 dorsocentral seta . . . . . *Nemopoda* Robineau-Desvoidy
11. Scutum (viewed dorsally) approximately as broad as long; fore coxa with osmeterium (Fig. 11) . . . . . *Diploosmeteriosepsis* Ozerov
– Scutum (viewed dorsally) approximately ½ as broad as long; fore coxa without osmeterium 12
12. Head with fronto-orbital setae (as in Fig. 5) 13
– Head without fronto-orbital setae 15
13. Mid tibia without ventral seta; wing veins R_{4+5} and M_1 convergent; costal vein (C) between veins R_{4+5} and M_1 shorter than *dm–m* crossvein (Fig. 16) . . . . . *Afronemopoda* Ozerov
– Mid tibia with 1 ventral seta; wing veins R_{4+5} and M_1 virtually parallel; costal vein (C) between veins R_{4+5} and M_1 approximately equal in length to *dm–m* crossvein (e.g., Fig. 23) 14
14. Head with postocellar setae; alula of wing entirely clothed in microtrichia . . . . . *Meroplius* Rondani [in part]
– Head without postocellar setae; alula of wing virtually bare, only clothed in microtrichia on ventral margin . . . . . *Xenosepsis* Malloch
15. Head with face narrow; antennal postpedicel wider than distance between eyes at level of vibrissae (Fig. 7) . . . . . *Afrosepsis* Ozerov
– Head with face broad; distance between eyes at level of vibrissae significantly wider than width of antennal postpedicel 16
16. Thorax with mediotergite grey pruinose 17
– Thorax with mediotergite at least shiny medially 18
17. Scutum with 1 dorsocentral seta . . . . . *Dudamira* Ozerov
– Scutum with 2 dorsocentral setae . . . . . *Leptomerosepsis* Duda

18. Head with 1 vibrissa (sometimes small); male fore femur with 2 or 3 black spines posteriorly (Fig. 30); male sternite 4 modified (Fig. 27); wing without black macula near apex of vein R_{2+3} (Fig. 23) . . . . . *Meroplius* Rondani [in part]

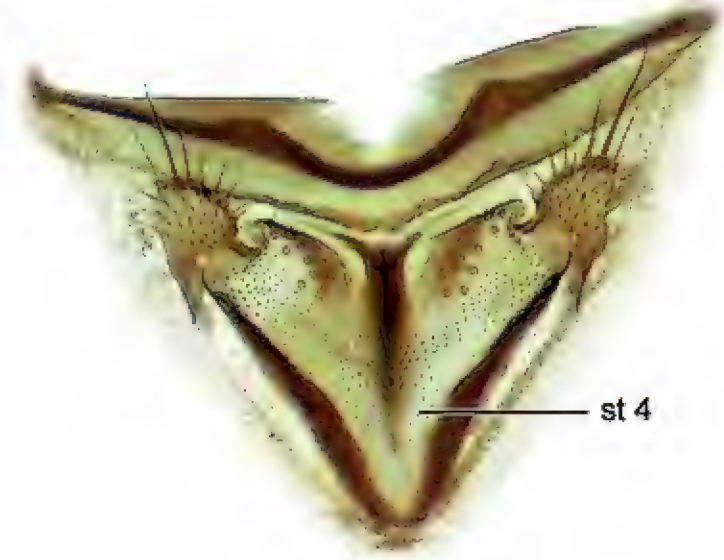
– Head with 2–4 vibrissae, invariably distinguishable from genal setulae; male fore femur with tubercles, stout spines or setae posteriorly (Figs 31, 32); sternite 4 simple (Fig. 28); wing often with black macula near apex of vein R_{2+3} (Fig. 17) . . . . . *Sepsis* Fallén [incl. *Lasiosepsis* Duda]

24 *Afromeroplius* ♂

25 *Dudamira* ♂



26 *Paratoxopoda* ♂



27 *Meroplius* ♂

28 *Sepsis* ♂

Figs 79.24–28. Male abdominal sternites of Sepsidae: (24) *Afromeroplius semlikiensis* (Vanschuytbroeck); (25) *Dudamira abyssinica* (Duda); (26) *Paratoxopoda barbata* Ozerov; (27) *Meroplius flavofemoratus* Ozerov; (28) *Sepsis delectabilis* Adams.

Abbreviation: st – sternite.

Synopsis of the fauna

Sepsidae occur in all zoogeographical regions of the world, except Antarctica. The world fauna currently comprises almost 350 species in 38 genera (Ang & Meier 2010; Ang *et al*. 2008; Iwasa 2007, 2008; Iwasa & Thinh 2008, 2012; Ozerov 2005, 2010, 2011, 2012, 2014). More than 120 species in 18 genera occur in the Afrotropical Region (Ozerov 2005, 2006, 2010, 2011, 2014).

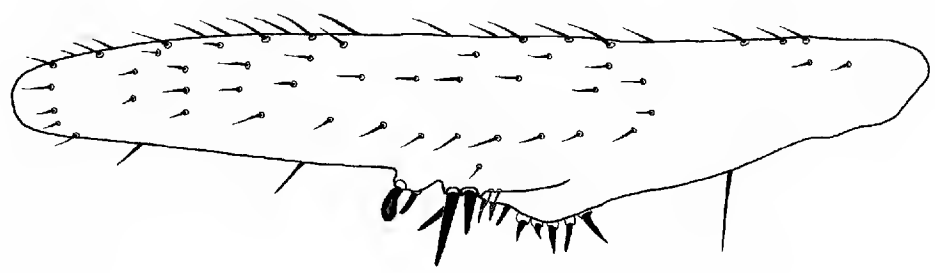
***Adriapontia* Ozerov.** An endemic genus of eight described species, ranging from Ethiopia to South Africa. Nothing is currently known regarding their habits and biology. The genus was revised and an identification key to species provided by Ozerov (2000*a*, 2014). High-quality photographs are included in the digital reference collection "SepsidNet" (http://sepsidnet-rmbr.nus.edu.sg/; Ang *et al*. 2013).

***Afromeroplius* Ozerov.** An endemic genus of two described species: *A. semlikiensis* (Vanschuytbroeck, 1963), recorded from Democratic Republic of Congo, Kenya and Namibia, swept from dung of African Bush Elephant, *Loxodonta africana* (Blumenbach) (Elephantidae) (Ozerov 2000*b*); and *A. watalingaensis* (Vanschuytbroeck, 1963), recorded only from Democratic Republic of Congo. The most recent identification key to species was provided by Ozerov (1996). High-quality photographs are included in the digital reference collection "SepsidNet" (http://sepsidnet-rmbr.nus.edu.sg/; Ang *et al*. 2013).

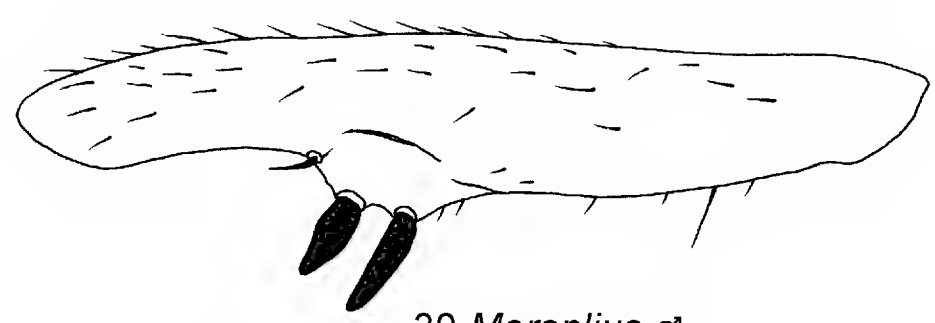
***Afronemopoda* Ozerov.** An endemic monotypic genus, with the single described species, *A. ealaensis* (Vanschuytbroeck, 1962), described from Democratic Republic of Congo (Vanschuytbroeck 1962) and further recorded from Uganda by Zuska (1977). Nothing is currently known regarding its habits and biology. High-quality photographs are included in the digital reference collection "SepsidNet" (http://sepsidnet-rmbr.nus.edu.sg/; Ang *et al*. 2013).

***Afrosepsis* Ozerov.** An endemic genus of six described species, recorded collectively from Angola, Cameroon, Ethiopia, Tanzania and Uganda (Ozerov 1999*a*, 2014). Nothing is currently known regarding their habits and biology. The genus was revised and an identification key to species provided by Ozerov (1999*a*). High-quality photographs of one species are included in the digital reference collection "SepsidNet" (http://sepsidnet-rmbr.nus.edu.sg/; Ang *et al*. 2013).

***Australosepsis* Malloch.** A small genus of three described species, occurring in the Afrotropical, Australasian/Oceanian, Oriental and Palaearctic Regions, one of which, *A. niveipennis* (Becker,

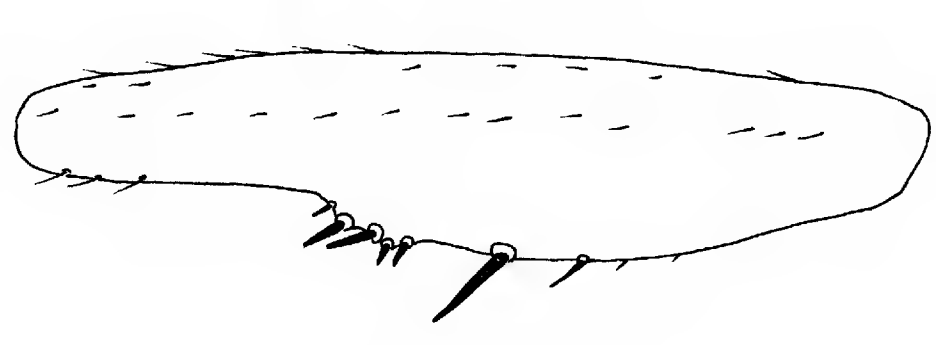


29 *Afromeroplius* ♂

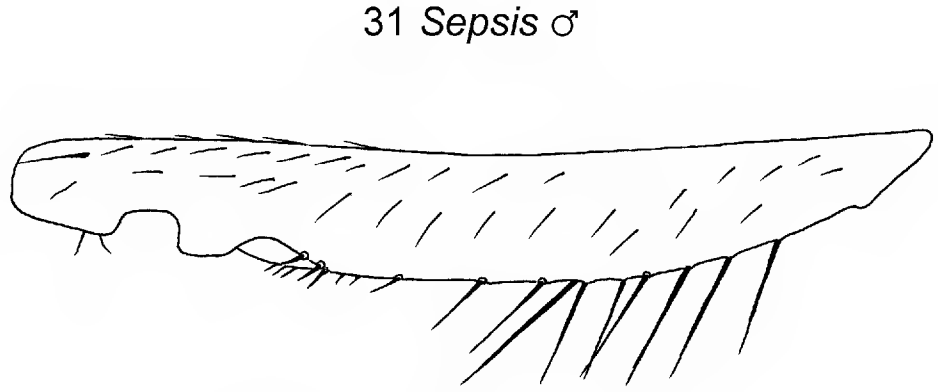


30 *Meroplius* ♂

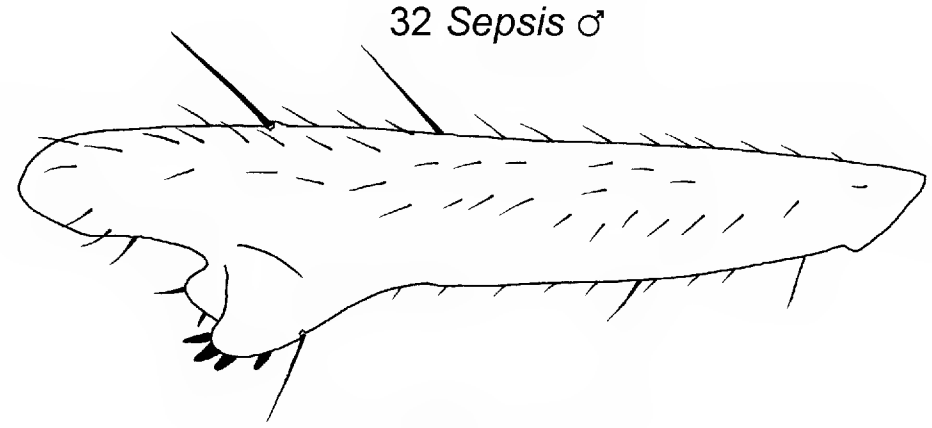
31 *Sepsis* ♂



32 *Sepsis* ♂



33 *Brachythoracosepsis* ♂



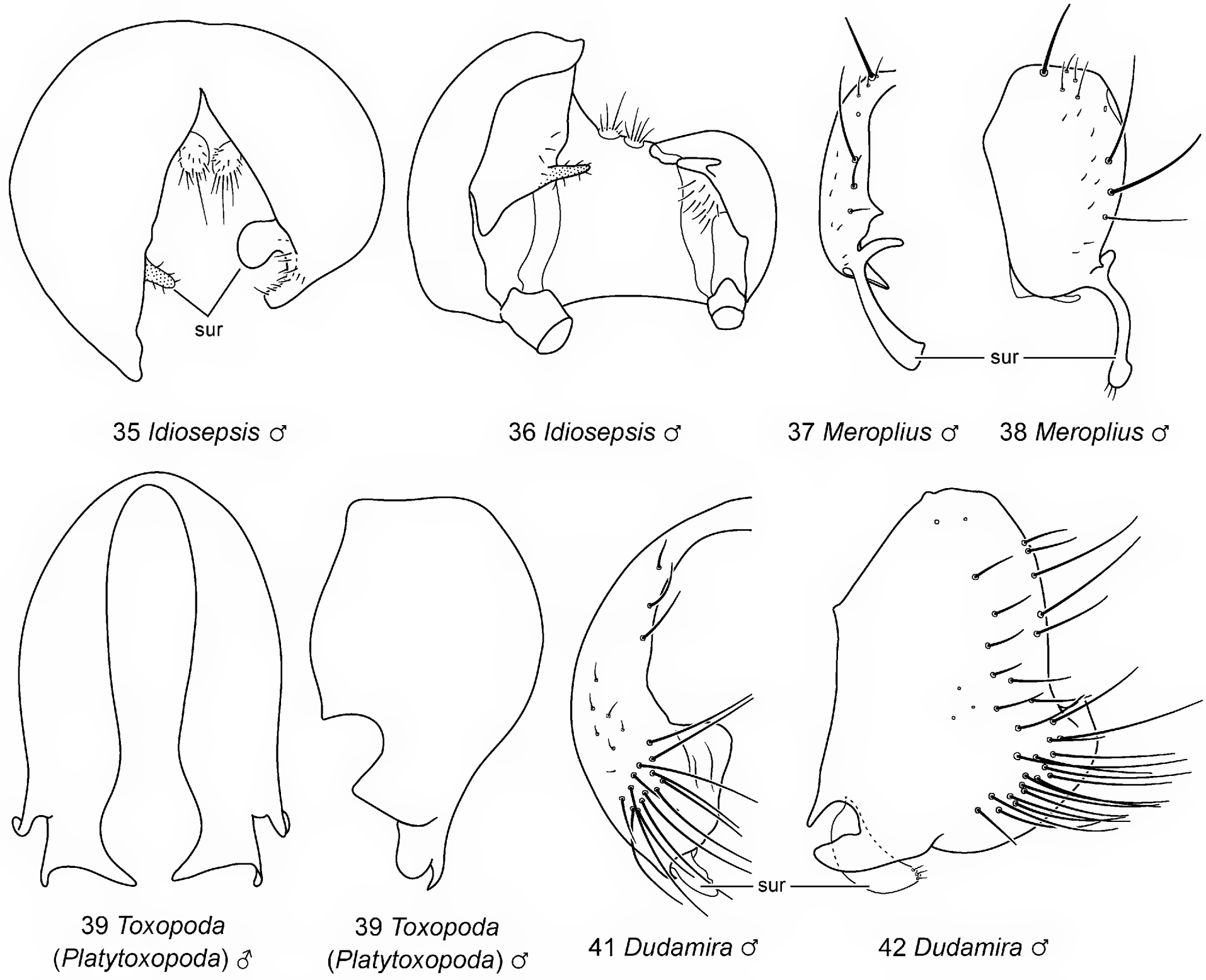
34 *Adriapontia* ♂

Figs 79.29–34. Male legs of Sepsidae (posterior views): (29) left fore femur of *Afromeroplius semlikiensis* (Vanschuytbroeck); (30) same, *Meroplius kirkspriggsi* Ozerov; (31) same, *Sepsis delectabilis* Adams; (32) same, *S. namibica* Ozerov; (33) same, *Brachythoracosepsis saotomensis* Ozerov; (34) same, *Adriapontia capensis* (Hennig). Fig. 29 (Ozerov 1996, fig. 2), Fig. 30 (Ozerov 2000*b*, fig. 30), Fig. 32 (Ozerov 2000*b*, fig. 9), Fig. 33 (Ozerov 2000*c*, fig. 6:1), Fig. 34 (Ozerov 2000*a*, fig. 1.1).

1903), is widespread in the Afrotropical Region. The genus is often synonymised with *Sepsis* (Lei *et al*. 2013; Pont & Meier 2002). Adults have been collected from dung of the African Bush Elephant in Namibia (Ozerov 2000*b*). The most recent identification key to species was provided by Iwasa (2007). High-quality photographs are included in the digital reference collection "SepsidNet" (http://sepsidnet-rmbr.nus.edu.sg/; Ang *et al*. 2013).

***Brachythoracosepsis* Ozerov.** An endemic genus of seven described species, three of which, *B. butikensis* (Vanschuytbroeck, 1963), *B. nodosa* (Walker, 1849) and *B. ruanoliensis* (Vanschuytbroeck, 1963), are widespread. They have been collected from a range of substrates, from herbivorous, carnivorous and omnivorous excrement (R. Meier, pers. comm. 2014). No identification key to species is currently available. High-quality photographs of five species are included in the digital reference collection "SepsidNet" (http://sepsidnet-rmbr.nus.edu.sg/; Ang *et al*. 2013).

***Dicranosepsis* Duda.** A genus that occurs predominantly in the Oriental Region, but with two described species in the Afrotropical Region: the widespread *D. takoensis* (Vanschuytbroeck, 1963) and *D. pallidispinifera* (Ozerov, 1999), only recorded from Uganda. Adults occur on cattle dung. An identification key to species, including the Afrotropical *D. takoensis*, was provided by Ozerov (2006). High-quality photographs of one Afrotropical species are included in the digital reference collection "SepsidNet" (http://sepsidnet-rmbr.nus.edu.sg/; Ang *et al*. 2013).



35 *Idiosepsis* ♂ 36 *Idiosepsis* ♂ 37 *Meroplius* ♂ 38 *Meroplius* ♂

39 *Toxopoda* (*Platytoxopoda*) ♂ 39 *Toxopoda* (*Platytoxopoda*) ♂ 41 *Dudamira* ♂ 42 *Dudamira* ♂

Figs 79.35–42. Male terminalia of Sepsidae: (35) epandrium and surstylus of *Idiosepsis spangleri* Ozerov, dorsal view; (36) same, posterior view; (37) same, *Meroplius flavofemoratus* Ozerov, dorsal view; (38) same, lateral view; (39) same, *Toxopoda* (*Platytoxopoda*) *nigrifoveata* Ozerov, dorsal view; (40) same, lateral view; (41) same, *Dudamira abyssinica* (Duda), dorsal view; (42) same, lateral view. Figs 35, 36 (Ozerov 1990, fig. 3), Figs 37, 38 (Ozerov 1999*b*, figs 9.6, 7), Figs 39, 40 (Ozerov 1991*a*, figs 4, 5), Figs 41, 42 (Ozerov 1996, figs 16, 18).

Abbreviation: sur – surstylus.

***Diploosmeteriosepsis* Ozerov.** An endemic monotypic genus, with the single species, *D. pilifemur* (Munari, 1994), described from Sierra Leone (Munari 1994) and further recorded from Nigeria by Ozerov (2005). Nothing is currently known regarding its habits and biology.

***Dudamira* Ozerov.** An endemic monotypic genus, with the single species, *D. abyssinica* (Duda, 1926), described from Ethiopia (Duda 1926*a*). Nothing is currently known regarding its habits and biology.

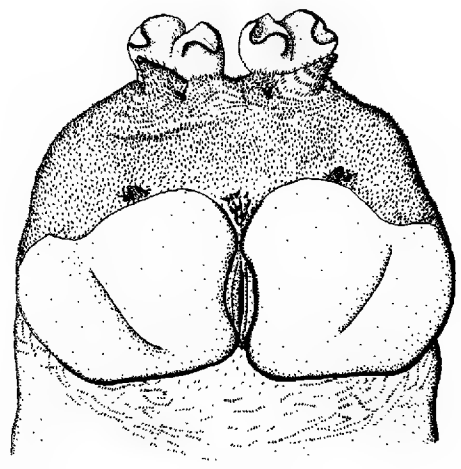
***Idiosepsis* Ozerov.** An endemic monotypic genus, with the single species, *I. spangleri* Ozerov, 1990, described from Uganda (Ozerov 1990). The presence of long dorsal branches on the antennal arista is the unique character of the genus (Fig. 6). Nothing is currently known regarding its habits and biology.

***Leptomerosepsis* Duda.** An endemic genus of four described species (Ozerov 2005). Nothing is currently known regarding their habits and biology. No key to species is currently available.

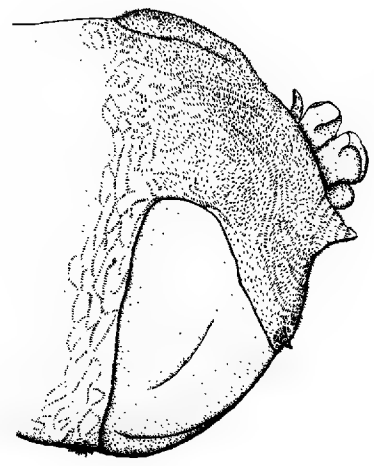
***Meroplius* Rondani.** A genus of 23 described species occurring in all zoogeographical regions, except Antarctica, 11 of which are recorded from the Afrotropical Region (Ozerov 2005, 2006). Adults of most described species have been collected from mammalian carrion. *Meroplius flavofemoratus* Ozerov, 2000 has been recorded from fresh African Bush Elephant dung in Namibia (Ozerov 2000*b*). Afrotropical species of this genus were revised and an identification key to species provided by Ozerov (1999*b*). Two additional Afrotropical species were described from Zambia (Ozerov 2011) and Ethiopia (Ozerov 2014). High-quality photographs of one Afrotropical species are included in the digital reference collection "SepsidNet" (http://sepsidnet-rmbr.nus.edu.sg/; Ang *et al*. 2013).

***Nemopoda* Robineau-Desvoidy.** A genus of three described species, occurring in the Afrotropical, Nearctic, Oriental and Palaearctic Regions, one of which, *N. nitidula* (Fallén, 1820) (Fig. 4), is recorded from Democratic Republic of Congo and may be introduced. Larvae appear to develop in mammalian carrion and excrement. The most recent identification key to species was provided by Ozerov (1997).

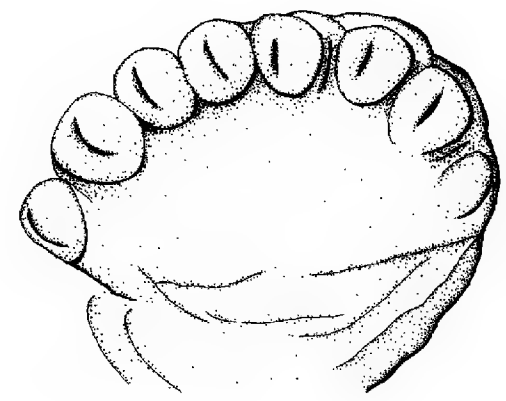
***Paratoxopoda* Duda.** An endemic genus of *ca* 30 described species. Medium-sized flies, usually with dark coloured bodies. The biology is largely unknown, although adults have been collected from antelope carrion in South Africa (Braack 1981)



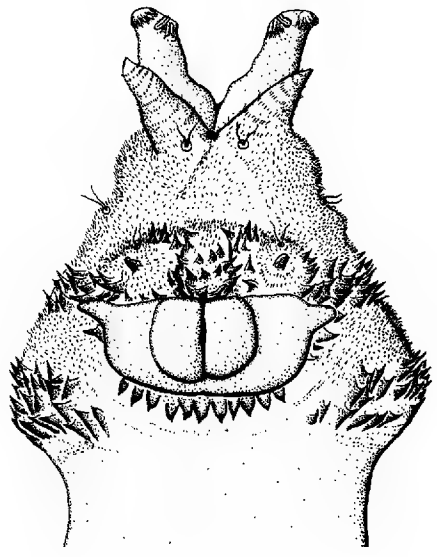
43 *Paratoxopoda*



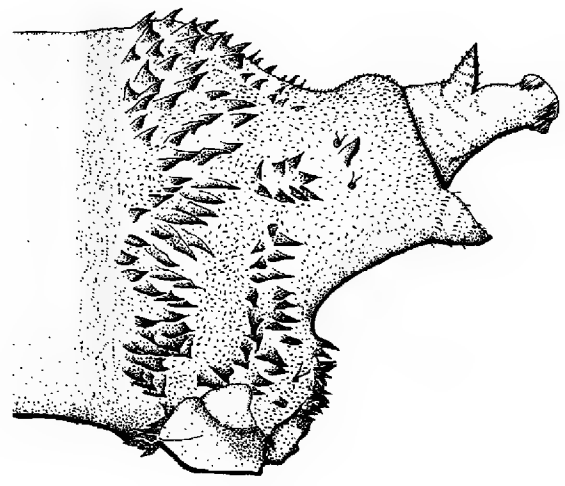
44 *Paratoxopoda*



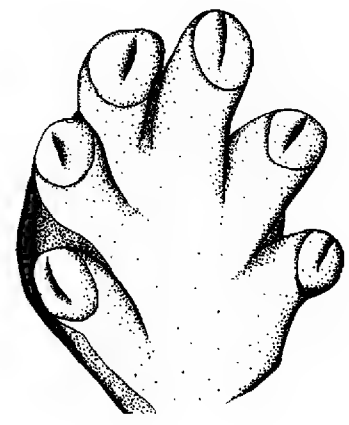
45 *Paratoxopoda*



46 *Sepsis*



47 *Sepsis*



48 *Sepsis*

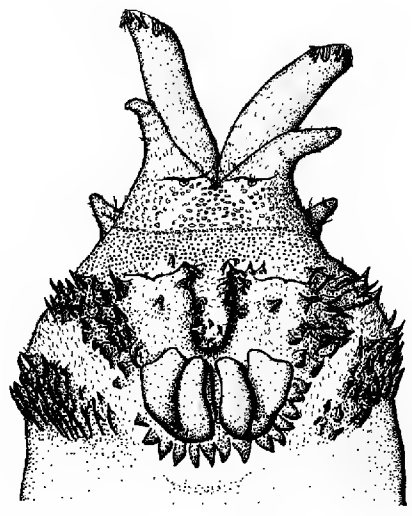
Figs 79.43–48. Third-instar larvae of Sepsidae: (43) abdominal segment 8 of *Paratoxopoda amonane* (Vanschuytbroeck), ventral view; (44) same, lateral view; (45) same, prothoracic spiracle, dorsal view; (46) abdominal segment 8 of *Sepsis lateralis* Wiedemann, ventral view; (47) same, lateral view; (48) same, prothoracic spiracle, dorsal view. Figs 43–45 (Meier 1996, figs 153–155), Figs 46–48 (Meier 1996, figs 269–271).

and from fresh African Bush Elephant dung in Namibia (Ozerov 2000*b*). *Paratoxopoda amonane* Vanschuytbroeck, 1961 was also collected from cattle dung in Zimbabwe by Meier (1996) and from dung of African buffalo, *Syncerus caffer* (Sparrman) (Bovidae) in South Africa (A.H. Kirk-Spriggs, pers. comm. 2016). The genus was revised and an identification key to species provided by Ozerov (1993). High-quality photographs for 12 species are included in the digital reference collection "SepsidNet" (http://sepsidnet-rmbr.nus.edu.sg/; Ang *et al*. 2013).

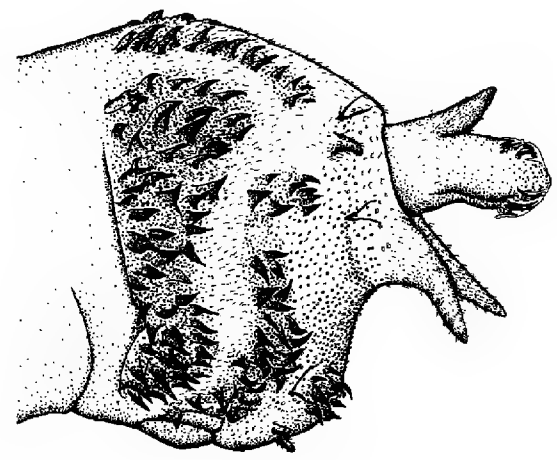
***Saltella* Robineau-Desvoidy.** A small genus of five described species occurring in the Afrotropical, Nearctic, Oriental and Palaearctic Regions. A single species, *S. bezzii* (Duda, 1926), is recorded from the Afrotropical Region, where it is widespread, but uncommon. This species has been recorded from dung of African buffalo in South Africa (A.H. Kirk-Spriggs, pers. comm. 2016). No identification key to species is currently available.

***Sepsis* Fallén.** The largest genus of Sepsidae with *ca* 90 species globally, occurring in the Afrotropical, Australasian/Oceanian, Nearctic, Neotropical (Costa Rica, Cuba, Mexico and Nicaragua), Oriental and Palaearctic Regions. Forty-three species are recorded from the Afrotropical Region, with numerous species with a dark macula at the apex of vein R_{2+3} (Fig. 17). Adults usually occur on domestic cattle dung. *Sepsis femoriseta* Duda, 1926, has been recorded from cattle dung in Zimbabwe (as Southern Rhodesia) (Cuthbertson 1937); *S. nigritarsis* Ozerov, 2000 and *S. namibica* Ozerov, 2000, from fresh African Bush Elephant dung in Namibia (Ozerov 2000*b*); *S. stenocalyptrata* Ozerov, 2004, from Rock hyrax, *Procavia capensis* (Pallas) (Procaviidae) droppings in South Africa (Ozerov 2004); and *S. thorcica* (Robineau-Desvoidy, 1830) from dung of domestic donkey, *Equus asinus* L. (Equidae), in South Africa (A.H. Kirk-Spriggs, pers. comm. 2016). Afrotropical species are in need of revision and no identification key to species is currently available. High-quality photographs of several species are included in the digital reference collection "SepsidNet" (http://sepsidnet-rmbr.nus.edu.sg/; Ang *et al*. 2013).

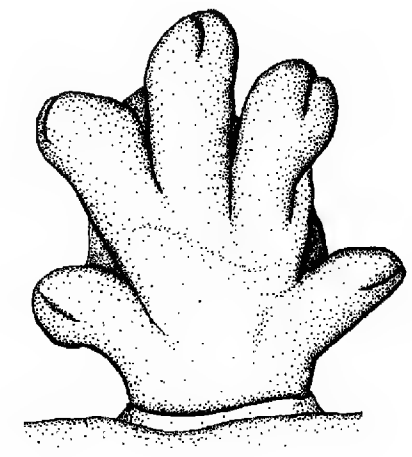
***Toxopoda* Macquart.** A genus of 17 described species globally occurring in the Afrotropical, Australasian/Oceanian, Oriental and Palaearctic (Egypt) Regions (Ozerov 2005). Two subgenera are recognised in the Afrotropical Region. *Toxopoda sensu stricto* (scutum with one dorsocentral seta), represented by the single species, *T.* (*T.*) *nitida* Macquart, 1851 widespread in the Afrotropical Region and further recorded from Egypt in the Palaearctic. The subgenus *Toxopoda* (*Platytoxopoda* Curran) (scutum with two dorsocentral setae), is represented by six endemic Afrotropical species. The genus has been collected from domestic cattle dung in Namibia (A.H. Kirk-Spriggs, pers. comm. 2013). An identification key to five species of *Platytoxopoda* was provided



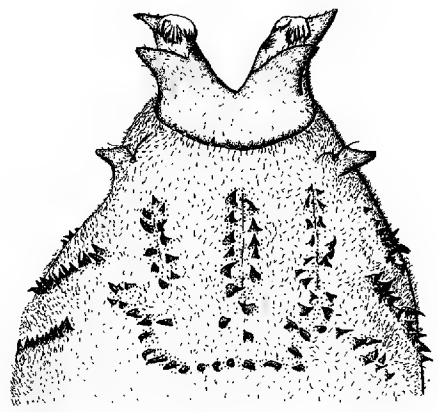
49 *Sepsis*



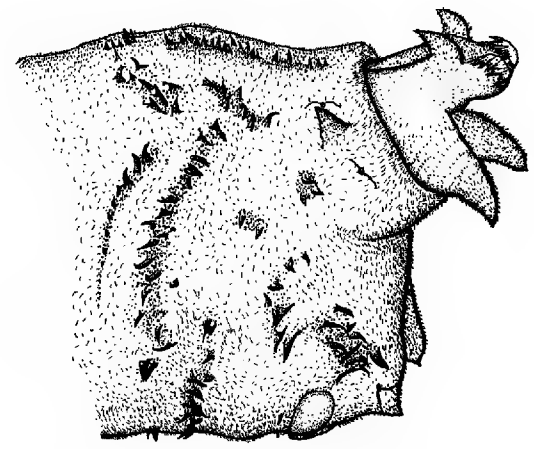
50 *Sepsis*



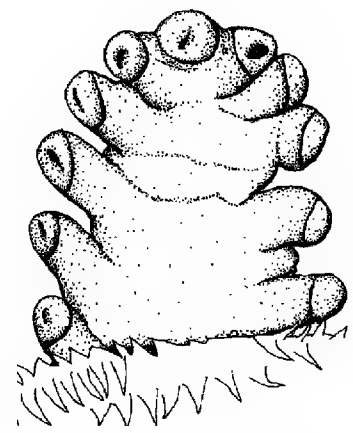
51 *Sepsis*



52 *Nemopoda*



53 *Nemopoda*



54 *Nemopoda*

Figs 79.49–54. Third-instar larvae of Sepsidae: (49) abdominal segment 8 of *Sepsis thoracica* (Robineau-Desvoidy), ventral view; (50) same, lateral view; (51) same, prothoracic spiracle, dorsal view; (52) abdominal segment 8 of *Nemopoda nitidula* (Fallén), dorsal view; (53) same, lateral view; (54) same, prothoracic spiracle, dorsal view. Figs 49–51 (Meier 1996, figs 341–343), Figs 52–54 (Meier 1996, figs 59–61).

by Ozerov (1991a). High-quality photographs of several species are included in the digital reference collection "SepsidNet" (http://sepsidnet-rmbr.nus.edu.sg/; Ang *et al*. 2013).

***Xenosepsis* Malloch.** A small genus represented by three described species globally. *Xenosepsis fukuharai* Iwasa, 1984 is widespread in the Palaearctic; *X. sydneyensis* Malloch, 1925, is recorded from the Australasian/Oceanian and Oriental Regions and *X. africana* (Ozerov) was described from Mozambique (Ozerov 1999*b*). Adults usually occur on mammalian carrion. No identification key to species is currently available. This genus is often synonymised with *Meroplius* and some species are included in the digital reference collection "SepsidNet" (http://sepsidnet-rmbr.nus.edu.sg/; Ang *et al*. 2013).

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NATALIMYZIDAE 80

(African Grass Flies)

David A. Barraclough

Fig. 80.1. Male of *Natalimyza* sp. (South Africa) (Kirk-Spriggs & Stuckenberg 2009, fig. 6.6).

Diagnosis

Moderately elongate, small-sized (body length: 2.5–4.5 mm) acalyptrate flies, without obvious sexual dimorphism, except in postabdomen; cuticle predominantly dull, pruinose; body colour yellow to brown (Fig. 1).

Head with palpus and proboscis well-developed (Fig. 1); fronto-orbital plate broad, with 2 large reclinate and 1 or 2 proclinate fronto-orbital setae (Figs 1–5); postocellar setae convergent (Fig. 5); face uniformly sclerotised; antennal pedicel without dorsal slit (Fig. 5); arista bare, inserted dorsolaterally on postpedicel (Fig. 5).

Thorax with prothorax very short, without sclerotised precoxal bridge; metathoracic postcoxal bridge absent; thoracic chaetotaxy: normally 4 dorsocentral setae (1 presutural); 1 + 1 notopleural setae; 2 pairs scutellar setae (basal pair reduced); 2–5 dorsal katepisternal setae; proepisternal and anepisternal setae lacking. Wing (Fig. 6) membrane hyaline, unmarked; costal vein (*C*) unbroken, other veins without macrotrichia; subcostal vein (*Sc*) complete, typically diverging from vein R_1 distally; vein R_{2+3} terminating close to apex of vein R_{4+5}; cells *dm*, *bm* and *cua* complete; cells *bm* and *cua* rounded distally; vein *CuA+CuP* vestigial beyond cell *cua*; vein A_1 visible well beyond alula, desclerotised; alula typically moderately developed. Legs with each tibia with 1 preapical dorsal seta; tarsi long and slender.

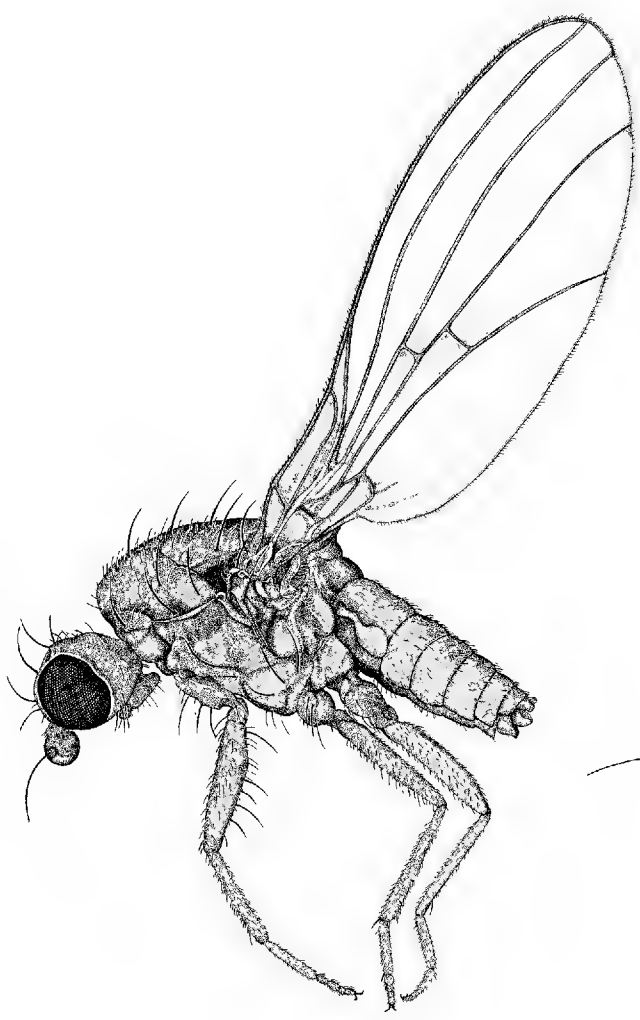
Abdomen with pre-abdominal spiracles in pleural membrane (Figs 7, 8); male pre-genital sclerites (protandrium) markedly asymmetrical, with tergite 6 and sternites 6, 7 and 8 well-developed (Figs 7, 8); surstylus fused to epandrium (Figs 9, 10); phallus, and particularly distiphallus, short (Figs 9–11); female: postabdomen simple, cerci separate (Figs 12, 13); 2 spermathecae (Fig. 14) (for further detail on the male and female postabdomen, refer to Barraclough & McAlpine (2006)).

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2021. Manual of Afrotropical Diptera. Volume 3. Brachycera—Cyclorrhapha, excluding Calyptratae. *Suricata* 8. South African National Biodiversity Institute, Pretoria; pp. 1861–1865.

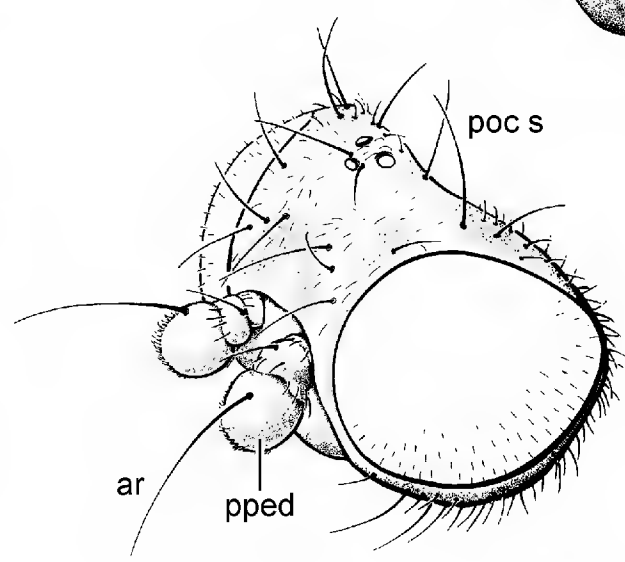
Adult Natalimyzidae are superficially similar to some species of Opomyzidae (see Chapter 84) and Chyromyidae (see Chapter 97), but the family is immediately distinguished by the unusual arrangement of the fronto-orbital setae (see above), the bare anepisternum, an unbroken costal vein (*C*) and the complete subcostal vein (*Sc*).

Biology and immature stages

Natalimyzidae are typically found in indigenous grassland. Although grassland is clearly the predominant habitat (based on current information), the family has also been recorded from indigenous Afromontane forests in the eastern provinces



2 *Natalimyza* ♀



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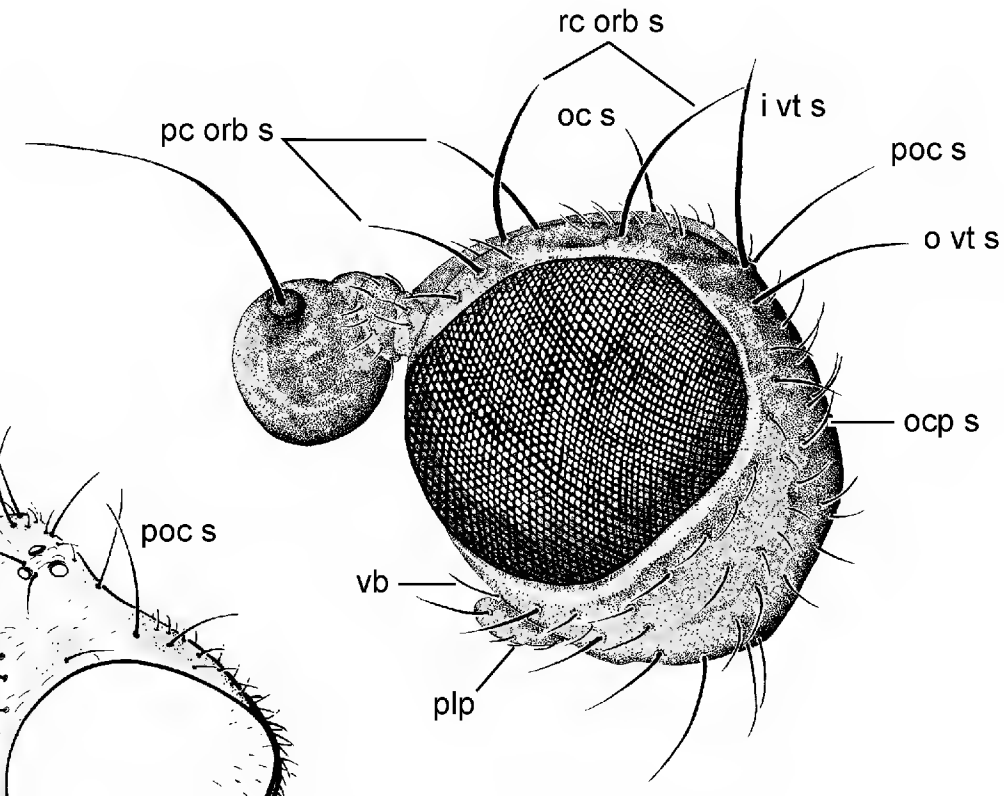

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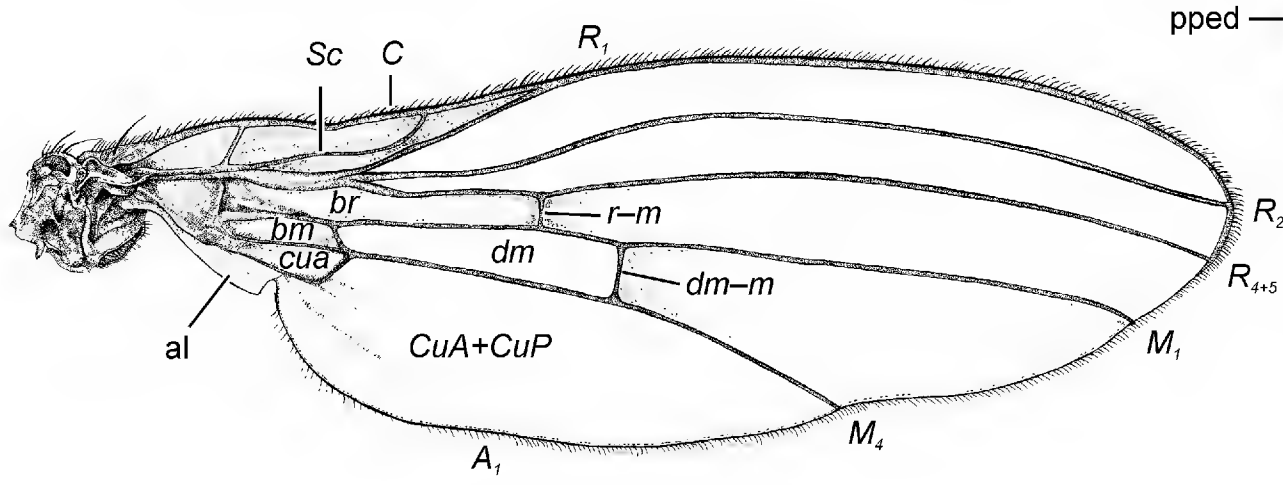
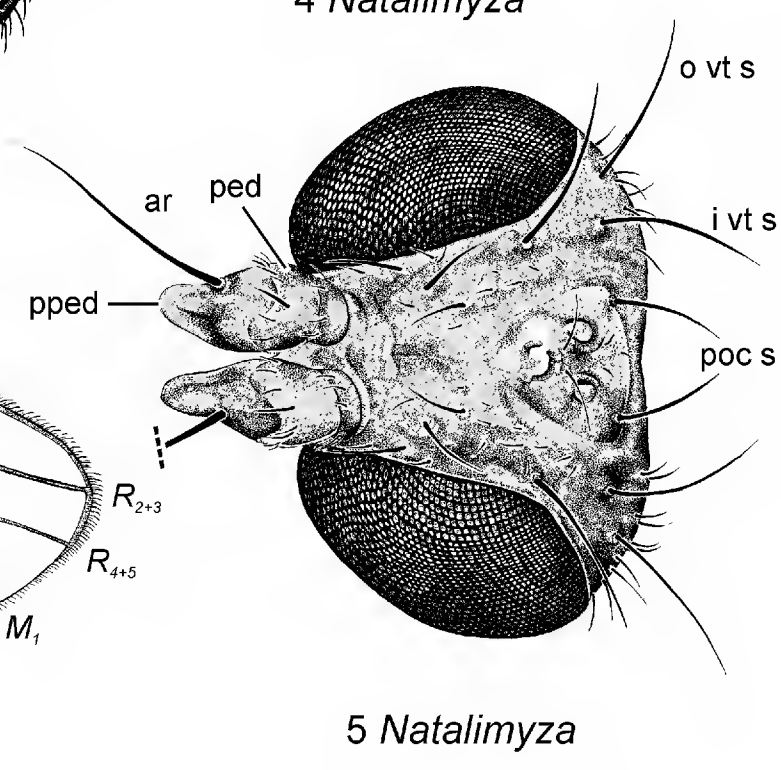


6 *Natalimyza*



5 *Natalimyza*

Figs 80.2–6. Habitus, heads and wing of Natalimyzidae: (2) habitus of *Natalimyza milleri* Barraclough & McAlpine, lateral view; (3) same, head, oblique view; (4) same, lateral view; (5) same, dorsal view (only base of left arista illustrated); (6) same, wing, dorsal view. Figs 2, 4–6 (Barraclough & McAlpine 2006, figs 1, 2–4), Fig. 3 (Barraclough 1995, fig. 24, as "New Family").

Abbreviations: A_1 – first branch of anal vein; al – alula; ar – arista; *bm* – basal medial cell; *br* – basal radial cell; *C* – costal vein; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *dm* – discal medial cell; *dm–m* – discal medial crossvein; i vt s – inner vertical seta; M_1 – first branch of media; M_4 – fourth branch of media; o vt s – outer vertical seta; oc s – ocellar seta; ocp s – occipital seta; pc orb s – proclinate orbital seta; ped – pedicel; plp – palpus; poc s – postocellar setae; pped – postpedicel; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; rc orb s – reclinate orbital seta; *r–m* – radial–medial crossvein; *Sc* – subcostal vein; vb – vibrissa.

of South Africa (Barraclough 2007; Kirk-Spriggs & Stuckenberg 2009: 173) and Mount Chirinda, Zimbabwe (Barraclough & McAlpine 2006). In South Africa, where the family has been most commonly collected to date, flies are usually taken during the dry, winter months in the eastern summer-rainfall region (Barraclough 2007; Barraclough & McAlpine 2006). The larvae appear to be micro-flora grazers on decaying grass, but have not been described. Miller (1984) reared the larvae, which are able to resist considerable desiccation, but none pupariated in laboratory rearings.

Natalimyzidae have been collected from a variety of habitats, ranging from coastal-dune vegetation, through to grassland at about 2,800 m (KwaZulu-Natal Drakensberg, South Africa) (Barraclough 2007; Barraclough & McAlpine 2006). Grassland species sometimes occur sympatrically and at a particular habitat there may be a succession of species through the seasons (Barraclough 2007). Highest abundance occurs during the dry winter months in eastern South Africa.

Economic significance

Natalimyzidae have no known economic significance.

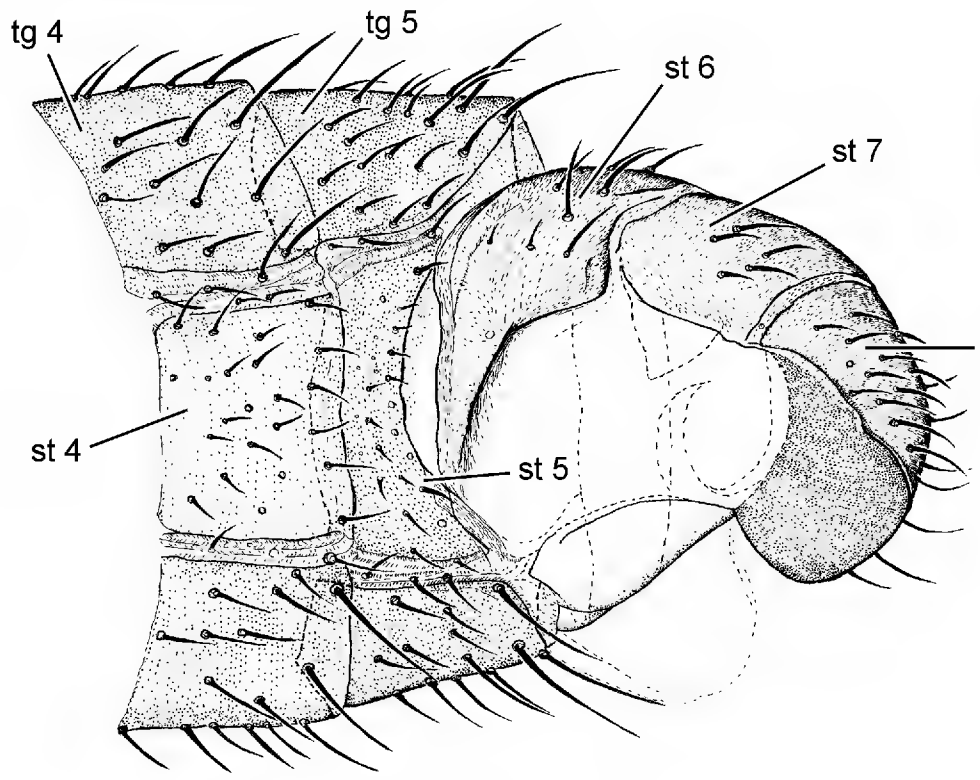
Classification

Natalimyza Barraclough & McAlpine, the only named genus in the family, possesses a character state combination which is more readily reconcilable with the Sciomyzoidea than with any other schizophoran superfamilies (Barraclough & McAlpine 2006). The family is treated as *incertae sedis* within the superfamily, pending a rigorous phylogenetic study of all included families and following further detailed taxonomic and phylogenetic studies of the Natalimyzidae (Barraclough & McAlpine 2006). Wiegmann *et al*. (2011) and Pape *et al*. (2011) also recently placed the Natalimyzidae as one of eight families in the Sciomyzoidea. Wiegmann *et al*. (2011), using data from a molecular analysis, placed them as a sister-group of the non-Afrotropical Heterocheilidae at the base of the superfamily.

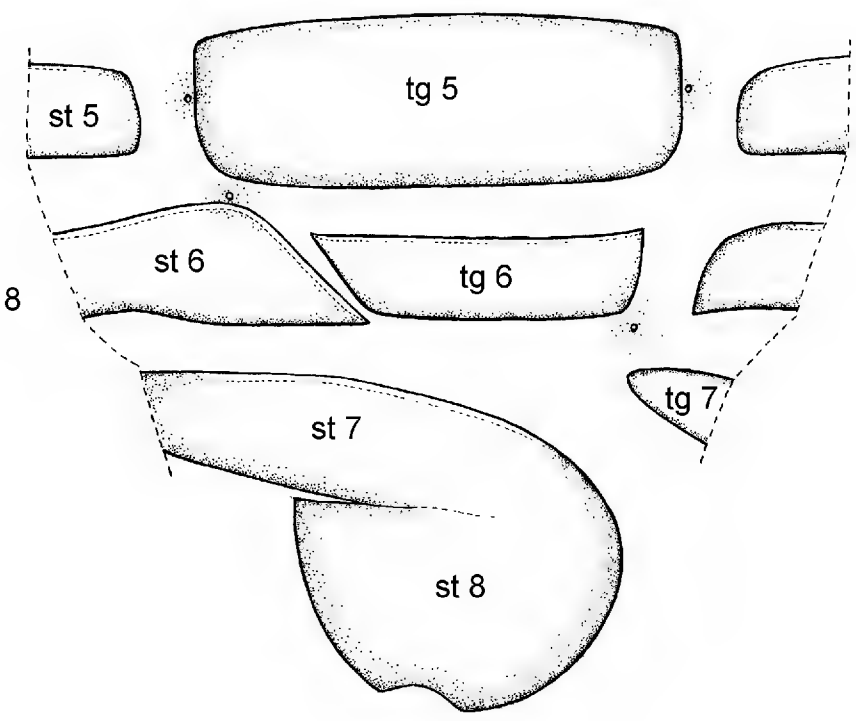
Identification

Barraclough (1995) was the first to formally distinguish the Natalimyzidae (as an undescribed "New family") in a key to all Southern African families of acalyptrate Diptera. The Natalimyzidae is the first widespread new family of Diptera described entirely from new Afrotropical taxa and the first new family of insects described from South African material since 1985 (Samways *et al*. 2012: 249).

The single genus *Natalimyza* appears to include two species-groups (Barraclough 2007; Barraclough & McAlpine 2006). The first comprises usually pallid species with the head and eye being depressed and the proboscis somewhat reduced in size. In these species the setae on the dorsal part of the head are typically reduced in length and strength. In the second group, to which the only named species (*Natalimyza milleri* Barraclough & McAlpine, 2006) in the family belongs, the head and eye are more or less rounded in profile and the proboscis is well-developed. In these species, the setae on the dorsal part of the head are elongate and well-developed. There are intermediate forms, however, and no generic distinction is warranted



7 *Natalimyza* ♂



8 *Natalimyza* ♂

Figs 80.7–8. Male postabdomen of Natalimyzidae: (7) pre-genital structures of *Natalimyza milleri* Barraclough & McAlpine, ventral view (detail of dorsal structures, including tergite 6, omitted); (8) same, protandrogram, ventral view (vestiture omitted). Figs 7, 8 (Barraclough & McAlpine 2006, figs 5, 6).

Abbreviations: st – sternite; tg – tergite.

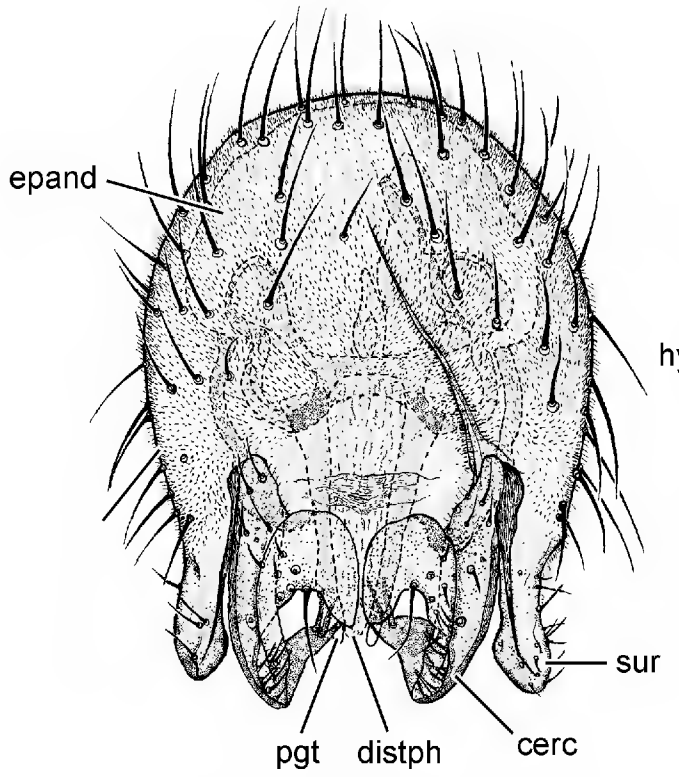
or possible at this stage. There is also significant intra-generic variation in the positioning of the *r–m* and *dm–m* crossveins, which are very closely approximated in some species, ranging through to relatively well-separated in others.

There are a host of characters of the male postabdomen that are useful for distinguishing and defining species. These include the shape and vestiture of the cercus (which may bear spines), the shape and vestiture of the epandrium; the shape of the surstylus; and the shape and vestiture of the hypandrium (sometimes with weakly developed spines).

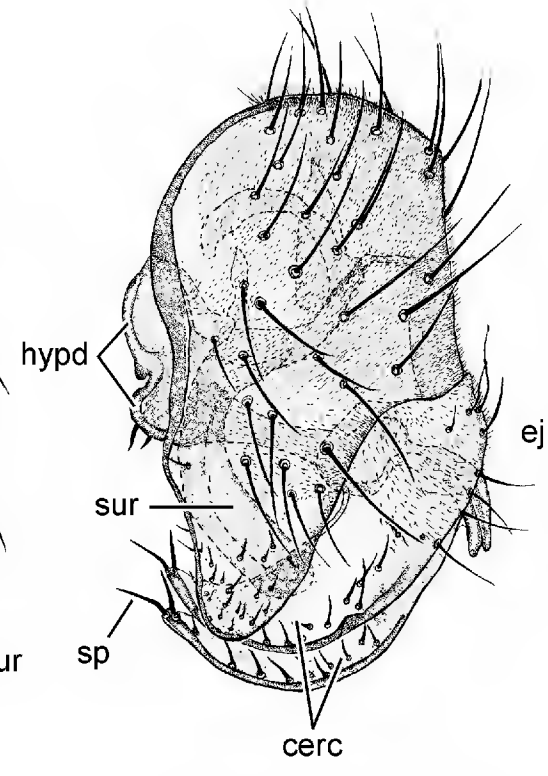
Although the extant Natalimyzidae is currently considered to be a family endemic to the Afrotropical Region – remarkably, it previously had a distribution in the Palaearctic Region. This is evidenced by a new species of *Natalimyza* recently recorded from Baltic amber (Eocene of Europe) (McAlpine 2011; Tschirnhaus & Hoffeins 2009). Natalimyzidae are best micro-pinned in the field for later double-mounting (see Chapter 2).

Synopsis of the fauna

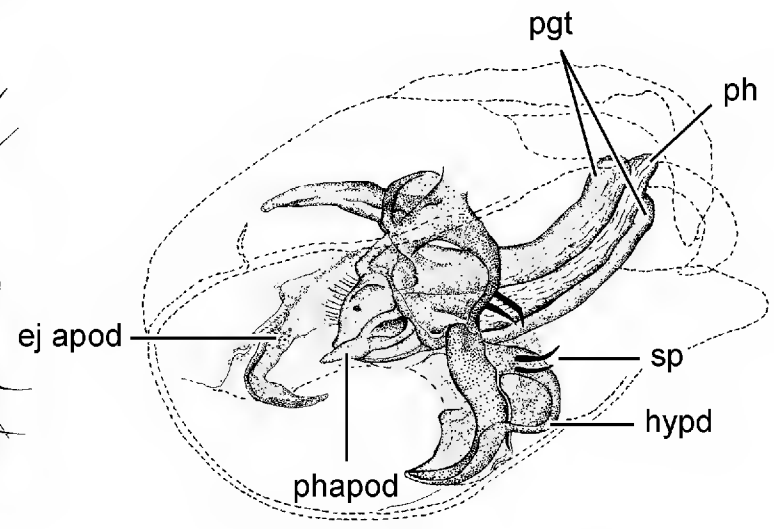
***Natalimyza* Barraclough & McAlpine.** The family is likely to be widespread and also relatively speciose in the Afrotropics, although it is represented only by the genus *Natalimyza*. A total fauna of more than 30 species could be expected, with



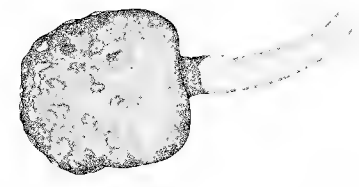
9 *Natalimyza* ♂



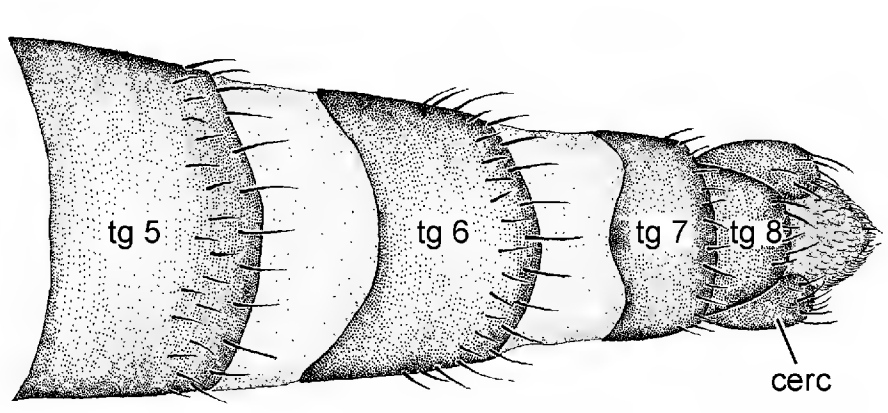
10 *Natalimyza* ♂



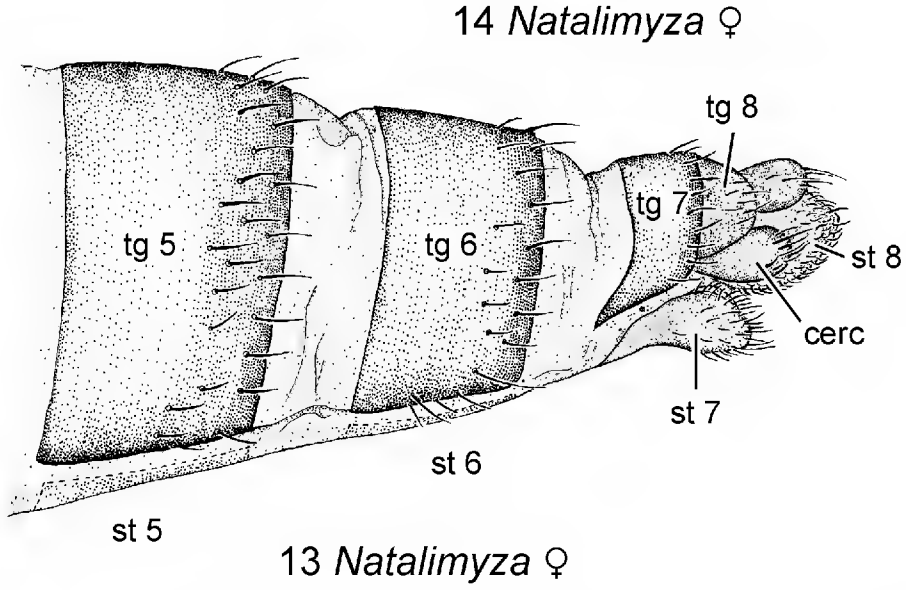
11 *Natalimyza* ♂



14 *Natalimyza* ♀



12 *Natalimyza* ♀



13 *Natalimyza* ♀

Figs 80.9–14. Male terminalia, female postabdomen and spermatheca of Natalimyzidae: (9) male terminalia of *Natalimyza milleri* Barraclough & McAlpine, dorsal view; (10) same, lateral view; (11) same, oblique ventral view; (12) same, female postabdomen, dorsal view; (13) same, oblique lateral view; (14) same, female spermatheca. Figs 9–14 (Barraclough & McAlpine 2006, figs 7–12).

Abbreviations: cerc – cercus; distph – distiphallus; ej apod – ejaculatory apodeme; epand – epandrium; hypd – hypandrium; pgt – postgonite; ph – phallus; phapod – phallapodeme; sp – spine; st – sternite; sur – surstylus; tg – tergite.

about 20 species present in South Africa alone (Barraclough & McAlpine 2006). The family is best known from southern and eastern South Africa and from Zimbabwe. It is also known from Nigeria and Kenya, although records from many additional Afrotropical countries should be expected. Natalimyzids are not expected to be present in Madagascar, owing to the secondary nature of much of the grassland there (Barraclough & McAlpine 2006).

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CLUSIIDAE 81

(Druid Flies)

Owen Lonsdale

Fig. 81.1. Male of *Heteromeringia* sp. (Madagascar) (photograph © S.A. Marshall).

Diagnosis

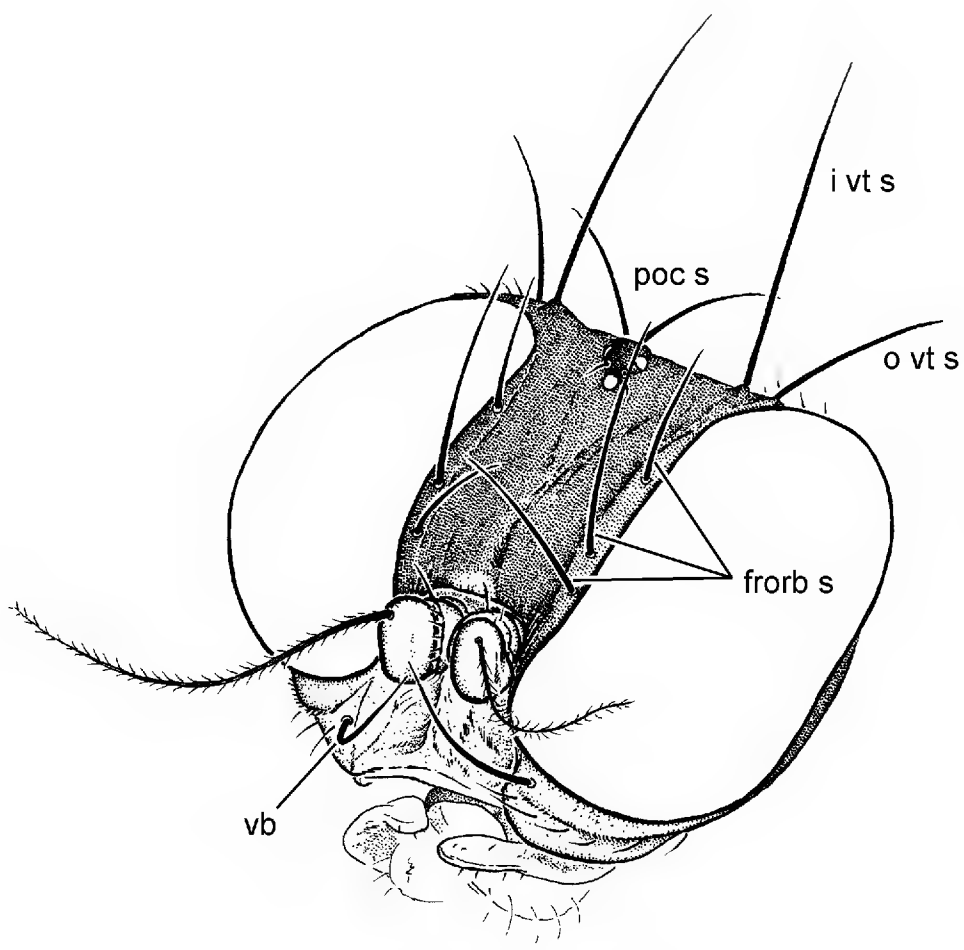
Small-sized, relatively slender acalyptrate flies (Fig. 1) (body length: *ca* 2.5–6.0 mm), with anterodistal margin of wing often infuscated and colouration varying from mainly black and brown (many *Czernyola* Bezzi *and Heteromeringia* Czerny), to almost entirely yellow or white (some *Sobarocephala* Czerny), but often with brown pattern on yellow background; antennal pedicel with angular process on outer and sometimes inner margins.

Head with antenna porrect; pedicel with angulate extension on outer and sometimes inner margins; antennal arista dorsoapical (not dorsobasal) (Figs 5, 6); face often soft and flat, sometimes lightly sclerotised, with dorsomedial surface produced as a shallow carina or bulge (Figs 2–4); 1 pair of pronounced vibrissae; ocellar and postvertical setae divergent when present; 2–5 fronto-orbital setae, if all setae reclinate, then either with (*Hendelia* Czerny) (Fig. 4) or without (*Allometopon* Kertész) interfrontal seta; anterior fronto-orbital seta sometimes inclinate (Sobarocephalinae, Clusiinae, *Heteromeringia*) (Fig. 2); if 4 or 5 setae present, then third posterior seta sometimes inclinate (*Czernyola*) (Fig. 3).

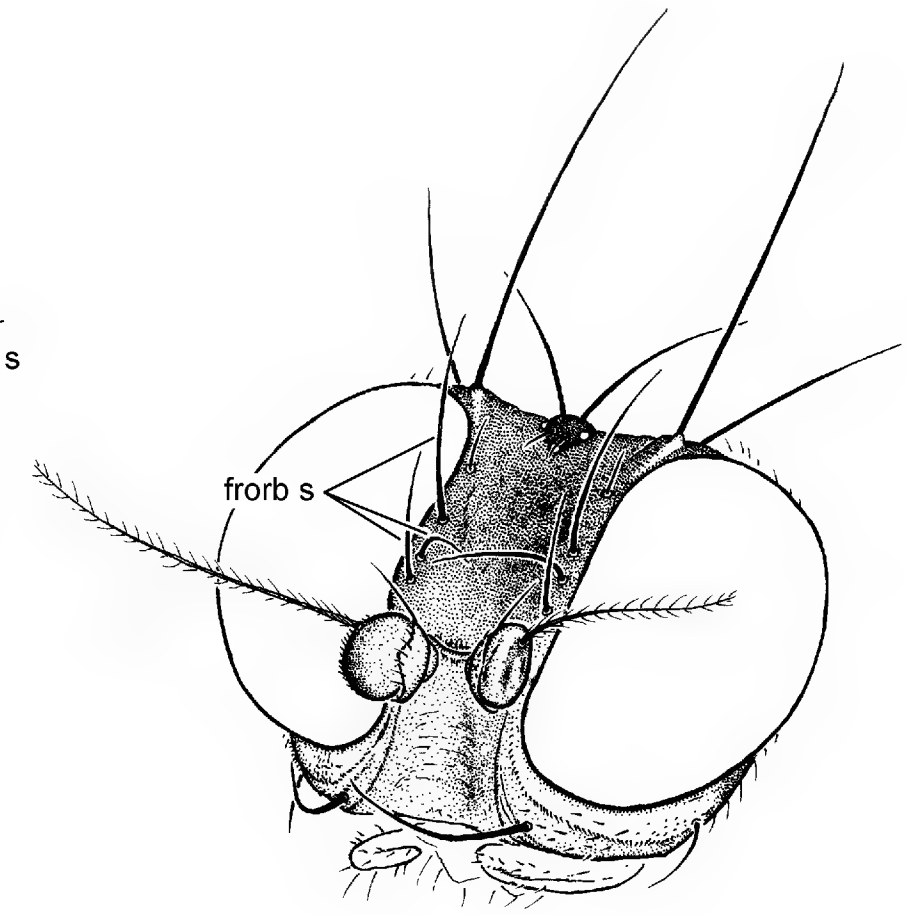
Thorax with 1 pronounced katepisternal and anepisternal seta; usually 2 or 3 dorsocentral setae; prosternum setulose. Legs with dorsal preapical tibial seta absent (*Allometopon, Heteromeringia*, *Tetrameringia* McAlpine), present on mid leg (*Sobarocephala*), or present on both mid and hind legs (*Czernyola*, *Hendelia*). Wing (Figs 7–12) with subcostal vein complete (Fig. 7); 1 costal break near insertion of subcosta (sometimes difficult to see in Clusiodinae); vein *CuA* complete, enclosing cell *cua* (anal cell); wing often infuscated, at least anterodistally (Figs 1–12); vein *CuA+CuP* well-developed.

Abdomen with male sternites 6 and 7 variably developed and left lateral to ventral; sternite 8 well-developed, dorsal to

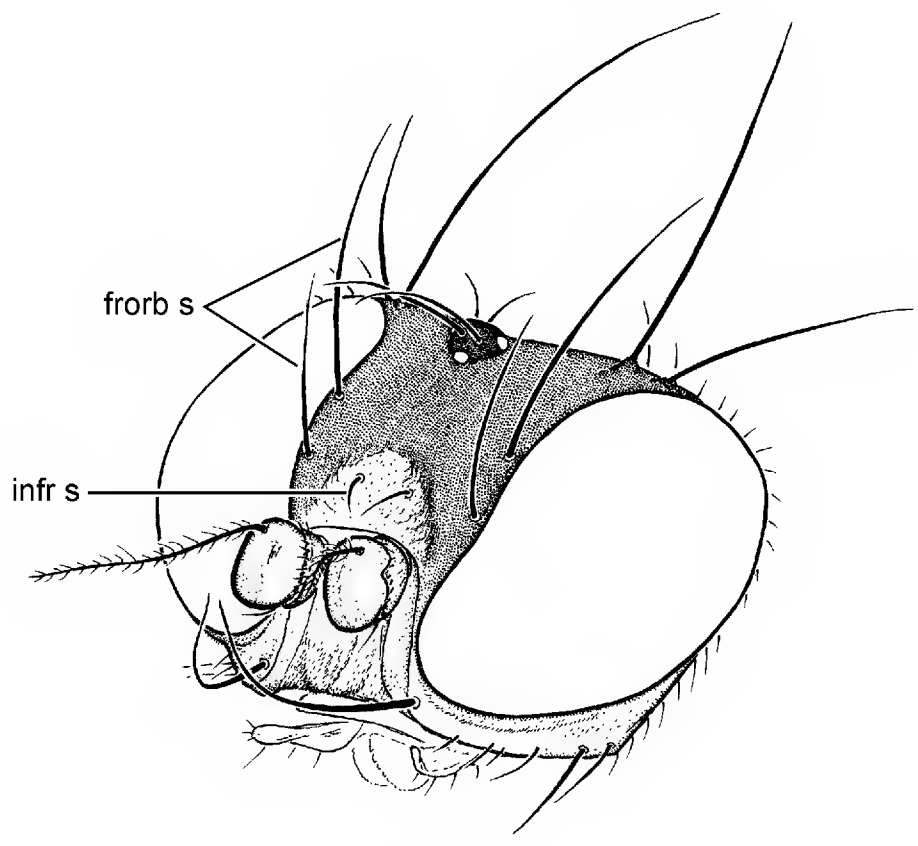
Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2021. Manual of Afrotropical Diptera. Volume 3. Brachycera—Cyclorrhapha, excluding Calyptratae. *Suricata* 8. South African National Biodiversity Institute, Pretoria; pp. 1867–1880.



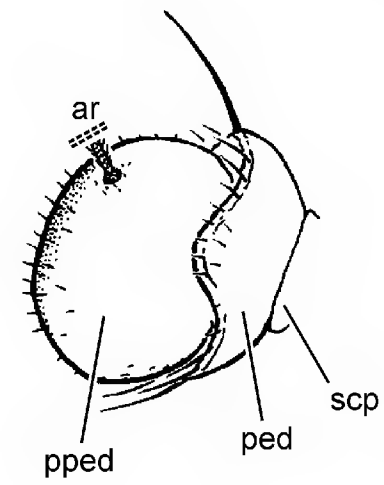
2 *Heteromeringia*



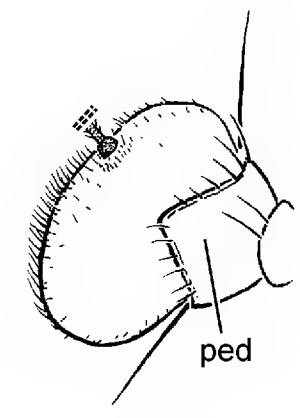
3 *Czernyola*



4 *Hendelia*



5 *Heteromeringia*



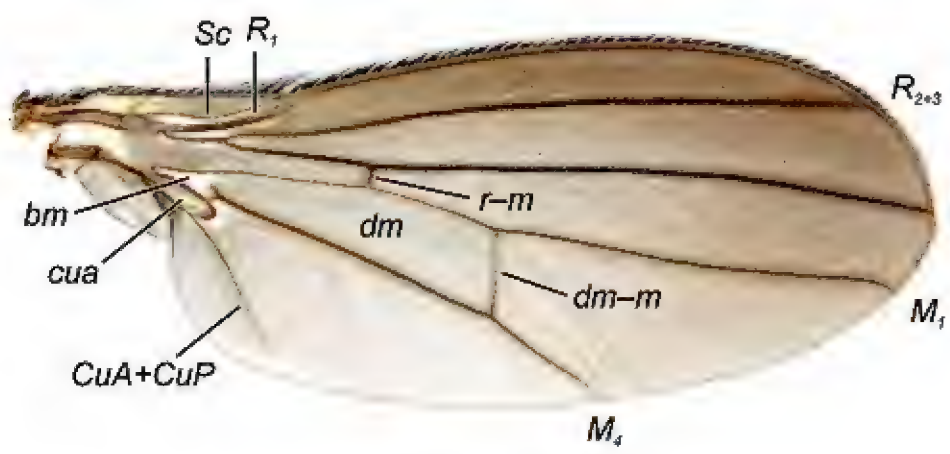
6 *Tetrameringia*

Figs 81.2–6. Heads and antennae of Clusiidae (dorsolateral views): (2) head of *Heteromeringia* sp.; (3) same, *Czernyola* sp.; (4) same, *Hendelia* sp.; (5) antenna, outer surface of *Heteromeringia* sp. (arista omitted); (6) same, *Tetrameringia* sp. (arista omitted).

Abbreviations: ar – arista; frorb s – fronto-orbital seta; i vt s – inner vertical seta; infr s – interfrontal seta; o vt s – outer vertical seta; ped – pedicel; poc s – postocellar seta; pped – postpedicel; scp – scape; vb – vibrissa.

right lateral; sternites 6–8 fused anteriorly, at least along left lateral margin, often forming complete ring through ventral fusion of sternites 6 and 8 (Figs 14, 23); tergite 7 small when present, forming sclerotised patch around right spiracle 7; female sternite 8 sometimes entire (Figs 37, 39), but usually apically bilobed and longitudinally divided (Fig. 35).

Some Chloropidae (see Chapter 96), Lauxaniidae (see Chapter 74), Psilidae (see Chapter 65) and non-Afrotropical Richardiidae have a superficially similar habitus and colouration, but these are otherwise readily differentiated. Other similarly narrow-bodied acalyptrates lack an angular projection on the antennal pedicel, with the following exceptions: Neriidae (see Chapter 63) have an extension only on the inner surface of the pedicel, but these are larger flies with veins R_{4+5} and M_1 convergent; Anthomyzidae (see Chapter 87) have the outer surface of the pedicel shallowly angulate, but the antenna is slightly elbowed, the postocellar setae are convergent or absent, the subcostal vein is incomplete and the fore femur usually has a ctenidial seta; Aulacigastridae (see Chapter 88) have extensions on both sides of the pedicel, but the inner process is more prominent and the subcostal vein is incomplete; Neminidae (see Chapter 89) also have a process only on the inner surface of the pedicel, but the anepisternal seta is highly reduced to absent and the subcostal vein is incomplete.



7 *Sobarocephala*

8 *Tetrameringia*

9 *Allometopon*

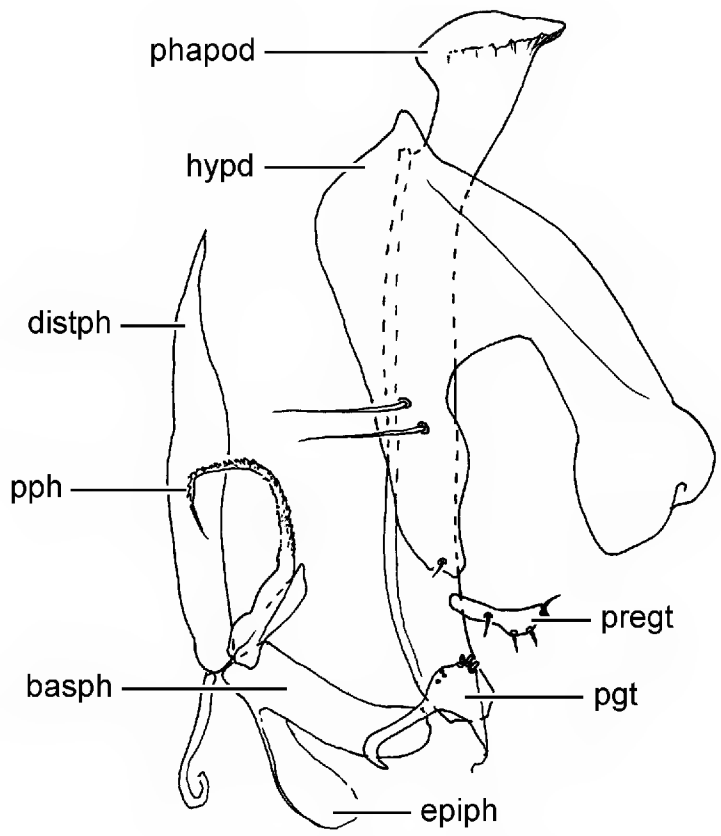
10 *Hendelia*

11 *Czernyola*

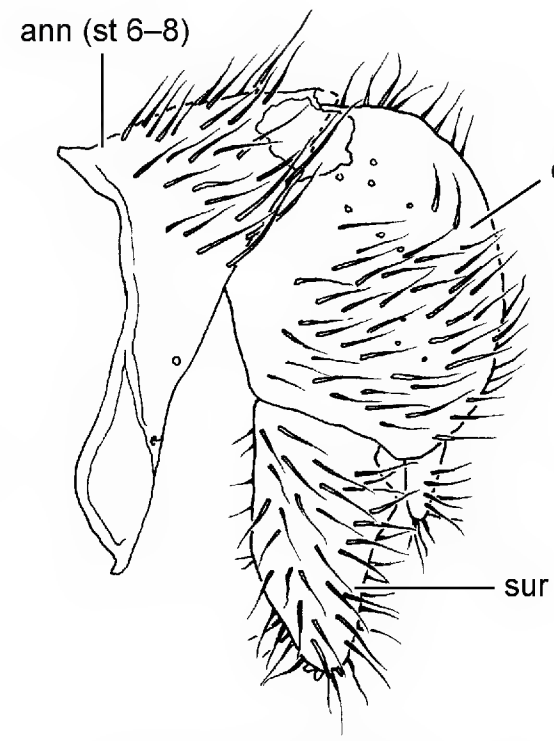
12 *Heteromeringia*

Figs 81.7–12. Wings of Clusiidae (dorsal views): (7) *Sobarocephala* sp.; (8) *Tetrameringia* sp.; (9) *Allometopon* sp.; (10) *Hendelia* sp.; (11) *Czernyola* sp.; (12) *Heteromeringia* sp.

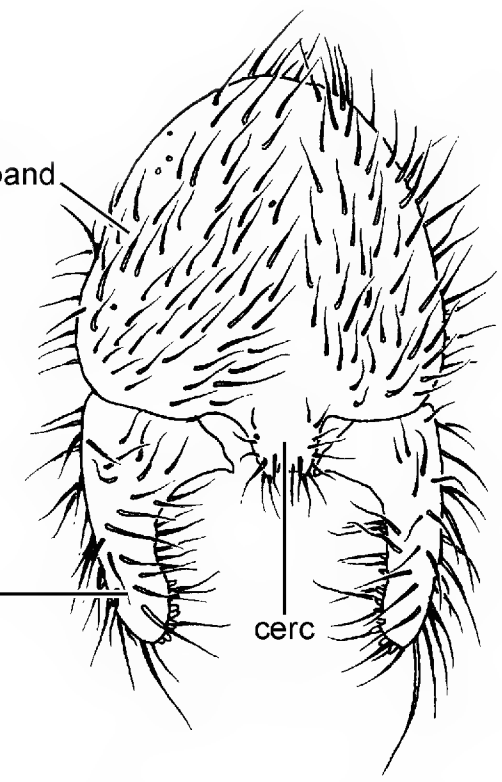
Abbreviations: *bm* – basal medial cell; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *dm* – discal medial cell; *dm–m* – discal medial crossvein; M_1 – first branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Sc* – subcostal vein.



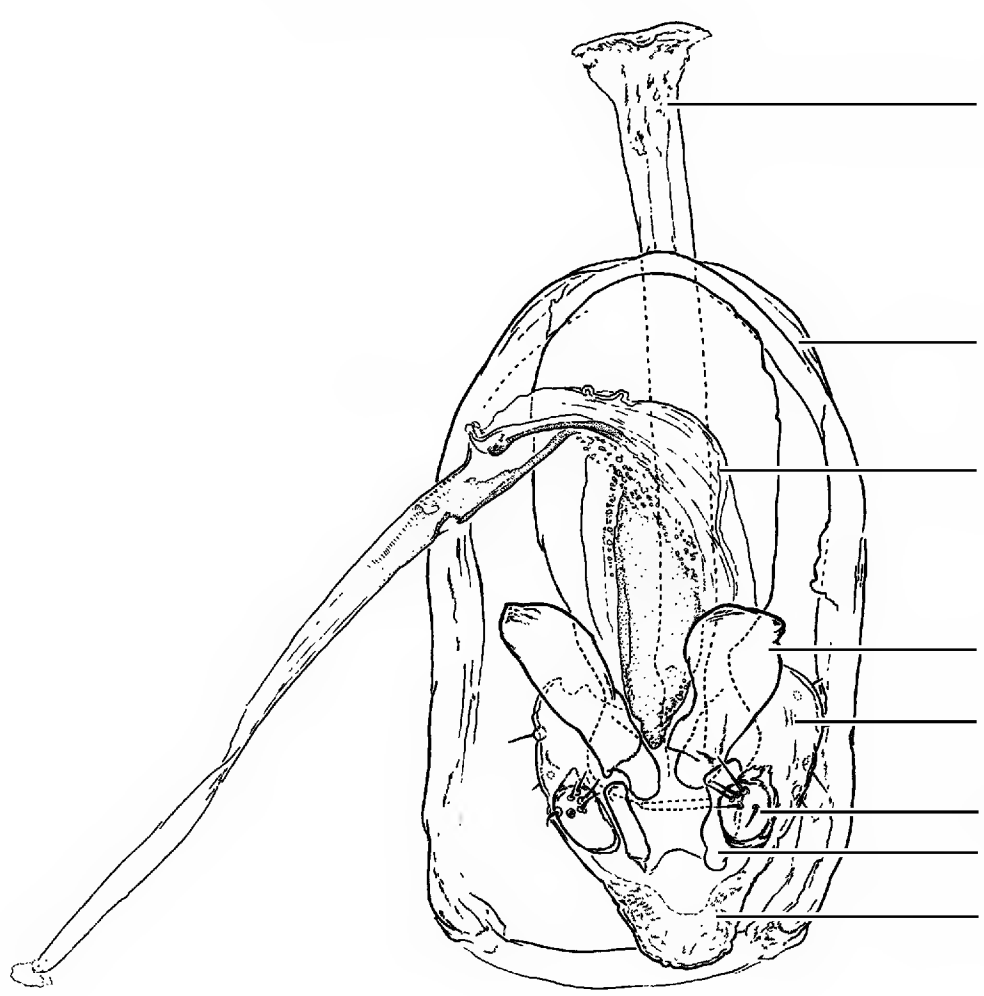
13 *Sobarocephala* ♂



14 *Sobarocephala* ♂



15 *Sobarocephala* ♂



16 *Tetrameringia* ♂

17 *Tetrameringia* ♂

Figs 81.13–17. Male terminalia of Clusiidae: (13) hypandrial complex of *Sobarocephala zuluensis* Stuckenberg, lateral view; (14) same, external components, lateral view; (15) same, posterior view; (16) hypandrial complex of *Tetrameringia* sp., ventral view; (17) same, lateral view, plus ejaculatory apodeme. Figs 13–15 (Lonsdale 2014, figs 66–68).

Abbreviations: ann (st 6–8) – annulus (sternites 6–8); basph – basiphallus; cerc – cerci (fused); distph – distiphallus; ej apod – ejaculatory apodeme; epand – epandrium; epiph – epiphallus; hypd – hypandrium; pgt – postgonite; phapod – phallapodeme; pph – paraphallus; pregt – pregonite; sur – surstylus.

Biology and immature stages

Adult Clusiidae are infrequently encountered in the field, although north temperate species can sometimes be collected with regularity in Malaise and pan traps in favoured habitats, such as partial grasslands and predominantly deciduous woodland. Conversely, mossy, humid habitats, often near waterways appear to be favoured in tropical regions. *Heteromeringia* species are more frequently encountered in open areas, such as tree falls, landslides and pastures (Lonsdale & Marshall 2010: 1043; Lonsdale *et al*. 2011).

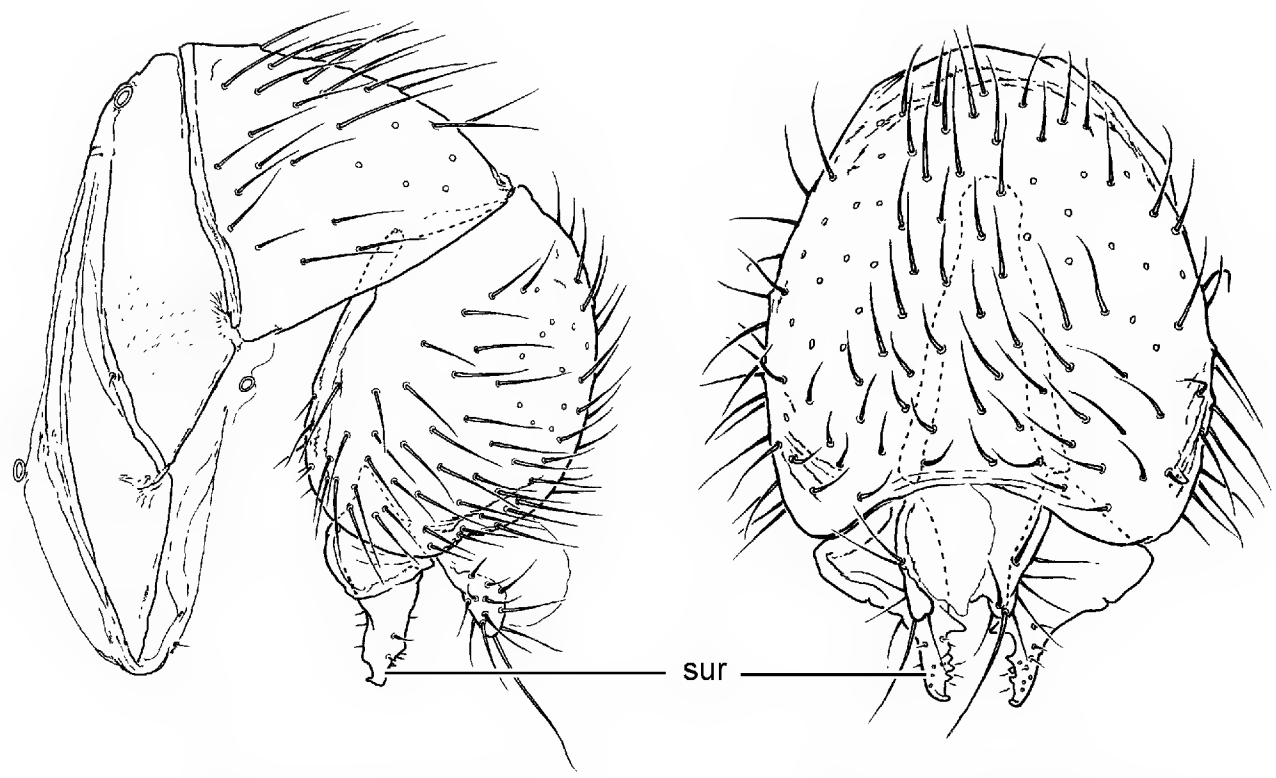
Within these habitats, individuals are often found in sunspots on the upper or lower surfaces of foliage. Adults are also often encountered on dead wood, such as stumps, fallen logs or branches, frequently in association with mammal or bird dung, but observations suggest that this behaviour may be less frequent in the New World tropics (Lonsdale & Marshall 2010: 1043). Adults have also been found on rotting meat (Caloren & Marshall 1998; Sasakawa 1998: 223) and are known to feed on fungal fruiting bodies (Caloren & Marshall 1998), nectar, rotting vegetable matter and sap (Soós 1987: 857). Many north temperate species have been found to develop within rotting wood, often under bark, and while several species are known from a single host species or genus, this may be a collecting artifact, as most other clusiids have been reared from a variety of deciduous and coniferous species (Caloren & Marshall 1998; Roháček 1995; Rotheray & Horsfield 2013; Withers 1985). Selection of oviposition sites by females does not appear to be associated with any particular species of tree, but is linked to "… humidity, amount of shade, stage of wood decay, [and the] presence of mycelia of certain fungi" (Roháček 1995: 124). While immatures appear to be more frequently recovered from wood in an advanced state of decay with soft whitewood (Rotheray & Horsfield 2013), some *Clusiodes* Coquillett have been found developing in freshly fallen trees (Caloren & Marshall 1998). Some *Sobarocephala* species have also been found in termite colonies (Sóos 1987: 857). Within the decaying wood, clusiid larvae appear to feed on biofilms through "spot sucking" actions and are unlikely to be predacious, due to their reduced cephaloskeleton and slow movement (Rotheray & Horsfield 2013). The position of larvae in fallen logs appears to be towards the underside of the wood between the annual rings and broken whitewood, but puparia are found towards the upper surface close to cracked bark or exposed inner wood; stump-inhabiting species also appear to pupariate towards the upper surface (Rotheray & Horsfield 2013).

Wood similar to, but less decayed than that selected for the larval habitat, is also used by species in all three subfamilies as a substrate for pre-copulatory and copulatory behaviour, although at least one species of Neotropical *Sobarocephala* uses the underside of broad leaves (Lonsdale & Marshall 2012). As part of pre-copulatory behaviour, clusiids are among the few acalyptrates known to establish leks, where the males defend territories within an arena devoid of resources from other lekking males, with females selecting males based on the "quality" of the territory held, leading to an asymmetry in reproductive success amongst males. True lekking, in this strict sense, has only been observed in the subfamily Clusiodinae (Caloren & Marshall 1998; Lonsdale & Marshall 2006*b*, 2007*b*; Marshall 2000), although territoriality and male agonistic behaviour has been observed in all subfamilies, and structural or colour modification associated with pre-copulatory display are present in all genera, particularly on the head, wings and fore legs (Lonsdale & Marshall 2010: 1043, 2012; Lonsdale *et al*. 2011, unpubl.; Marshall 2000). When males encounter each other in a lek, they appear to assess body size in an attempt to determine which male is largest, this male being the most likely to win in a violent confrontation. The larger male subsequently retains or gains control of the territory, avoiding unnecessary and costly physical confrontation. Violence usually occurs only when the males are of near equal size and it is uncertain which individual would win in a fight, although ambush attacks are also components of agonistic behaviour in some species (Caloren & Marshall 1998). It is assumed that leg and wing displays, widened heads, modified vibrissae, elongate antennae and other such visual components of pre-copulatory display exaggerate body size for more accurate measurement of fitness (Marshall 2000), although their utility in violent confrontation and male/female interaction may also be significant.

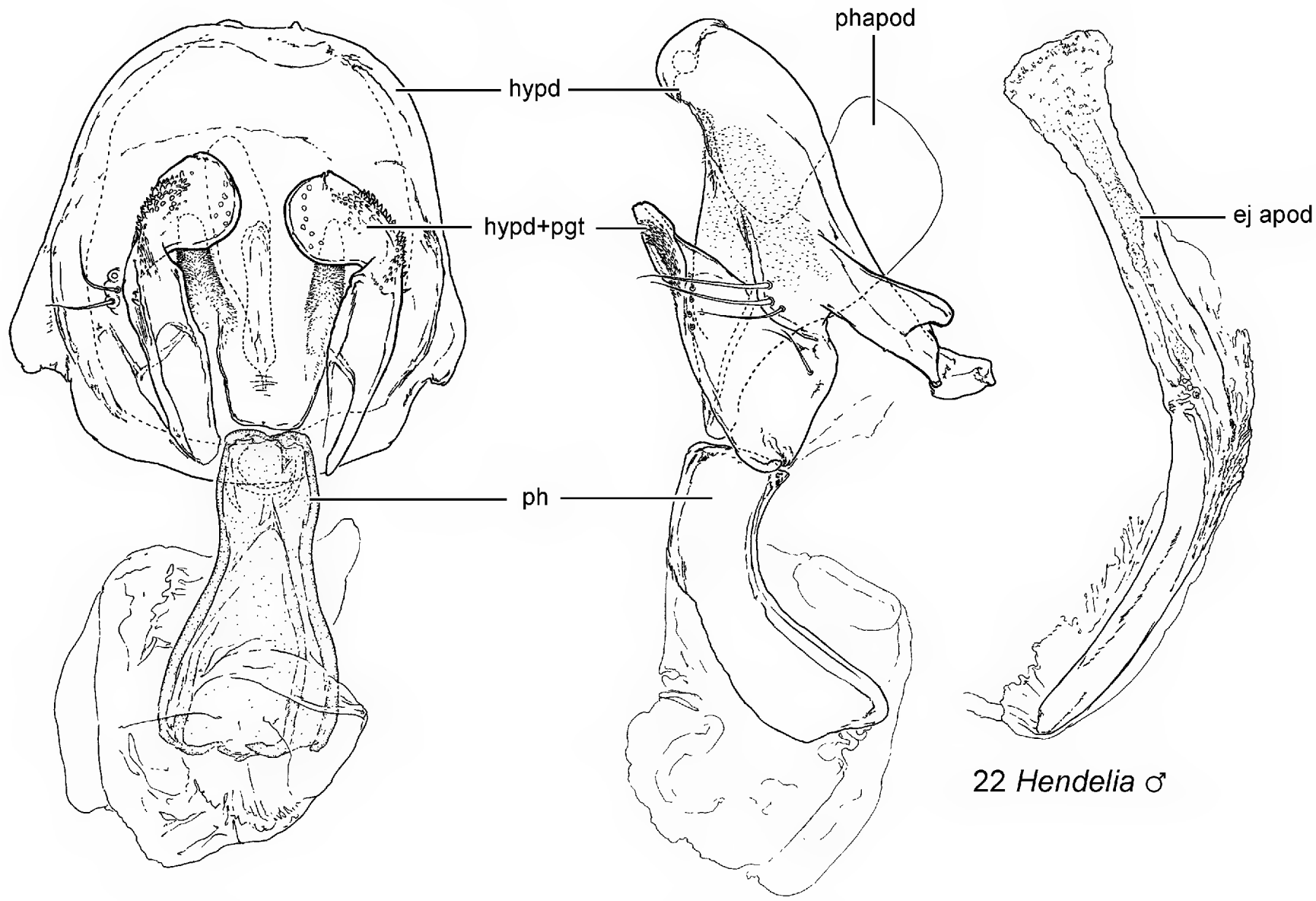
Immature stages are not known for Afrotropical species, but clusiid eggs described for genera that occur in the Afrotropics are approximately as long as female sternite 6, three or four times longer than wide, with a small, slightly raised terminal micropile and are tapered at both ends (Lonsdale 2009; Lonsdale & Marshall 2012; Lonsdale *et al*. 2011). The surface is translucent, usually tuberculate, with longitudinal wrinkles or furrows (Fig. 39, above).

Larvae have been described for species of European *Clusiodes* in Malloch (1918) and Soós (1987). Rotheray & Horsfield (2013) have more recently provided a comprehensive analysis of the immature stages of several Palaearctic *Clusia* Haliday and *Clusiodes* species. Described larvae are white and tapered at both ends, segmental boundaries are visible as raised, impressed or otherwise obvious lines; the prothorax is truncated with surrounding sensillae; the prothoracic spiracles are posterolateral on the prothorax, fan-shaped, with 3–10 respiratory papillae; the anal pad is pale and the posterior spiracles are elevated on sclerotised plates, which are produced as dorsally curving hooks; spiracular openings elongate-oval in radial pattern (Figs 43, 44). The mouthhooks are small and well-sclerotised and the cephaloskeleton is unpigmented, exhibiting significant reduction and fusion (Fig. 45). The pseudocephalon lacks a facial mask with cirri and the atrium is oblique (Rotheray & Horsfield 2013).

Puparia (Figs 42–44) are known from several species in all three subfamilies (Lonsdale 2009; Lonsdale & Marshall 2007*b*; Lonsdale *et al*. 2011; Sabrosky & Steyskal 1974) and several *Clusia* and *Clusiodes* species were treated thoroughly in Rotheray & Horsfield (2013). Puparia are dark brownish orange, with the anal pad darker and more heavily sclerotised. There are numerous minute transverse wrinkles, although the posterior segment is smooth with various sculpturing (wrinkles and divots) and is either sharply curved and bordered by a high ridge (*Clusia* and *Sobarocephala*), or broadly rounded with the ridge broken and shallow (*Clusiodes*). The hooked projections bearing the posterior spiracles either curve dorsally (*Clusiodes*), or medially to dorsomedially and are ovate (*Clusia* and *Heteromeringia*), or semicircular (*Sobarocephala*) in cross-section; the hooked projections of *Heteromeringia* species (known from Australian *H. norrisi* McAlpine, 1960 and Nearctic *H. nitida* Johnson, 1913 (Lonsdale, unpubl.)), have an additional pointed process medially.



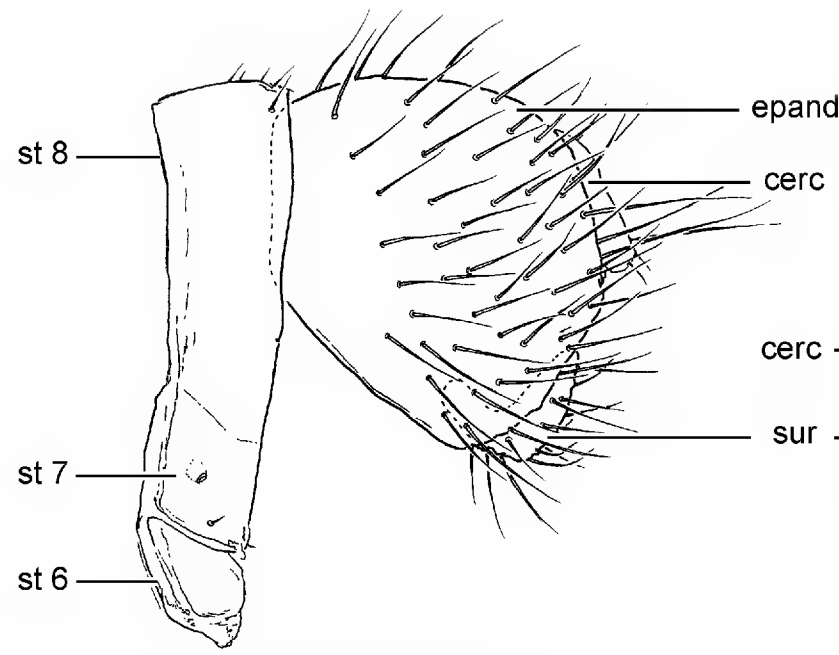
18 *Tetrameringia* ♂ 19 *Tetrameringia* ♂



20 *Hendelia* ♂ 21 *Hendelia* ♂ 22 *Hendelia* ♂

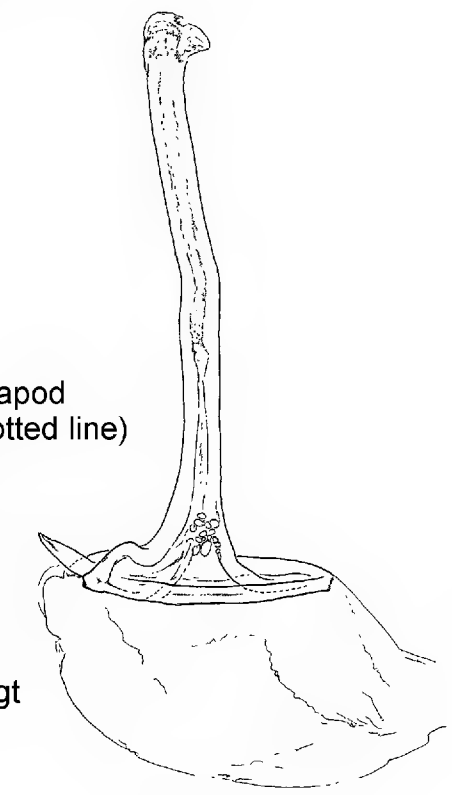
Figs 81.18–22. Male terminalia of Clusiidae: (18) external components of *Tetrameringia* sp., lateral view; (19) same, posterior view; (20) hypandrial complex of *Hendelia* sp., ventral view; (21) same, lateral view; (22) same, ejaculatory apodeme.

Abbreviations: ej apod – ejaculatory apodeme; hypd – hypandrium; pgt – postgonite; ph – phallus; phapod – phallapodeme; sur – surstylus.

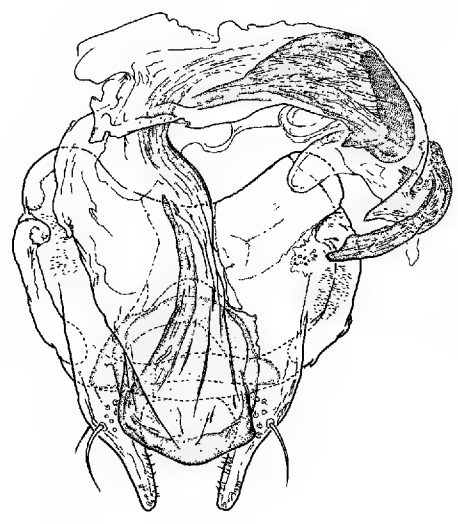


23 *Hendelia* ♂

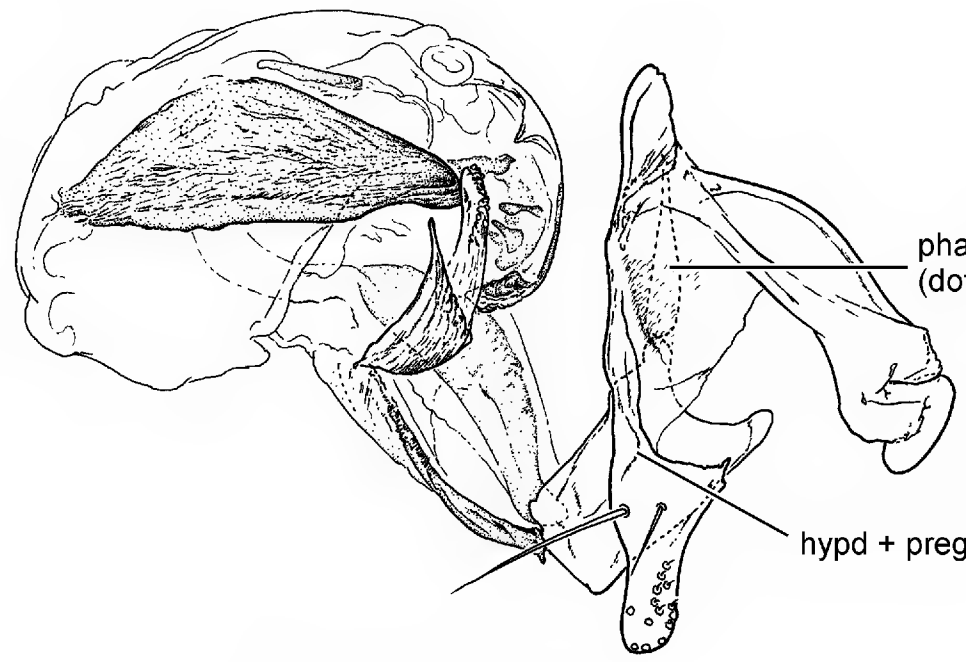
24 *Hendelia* ♂



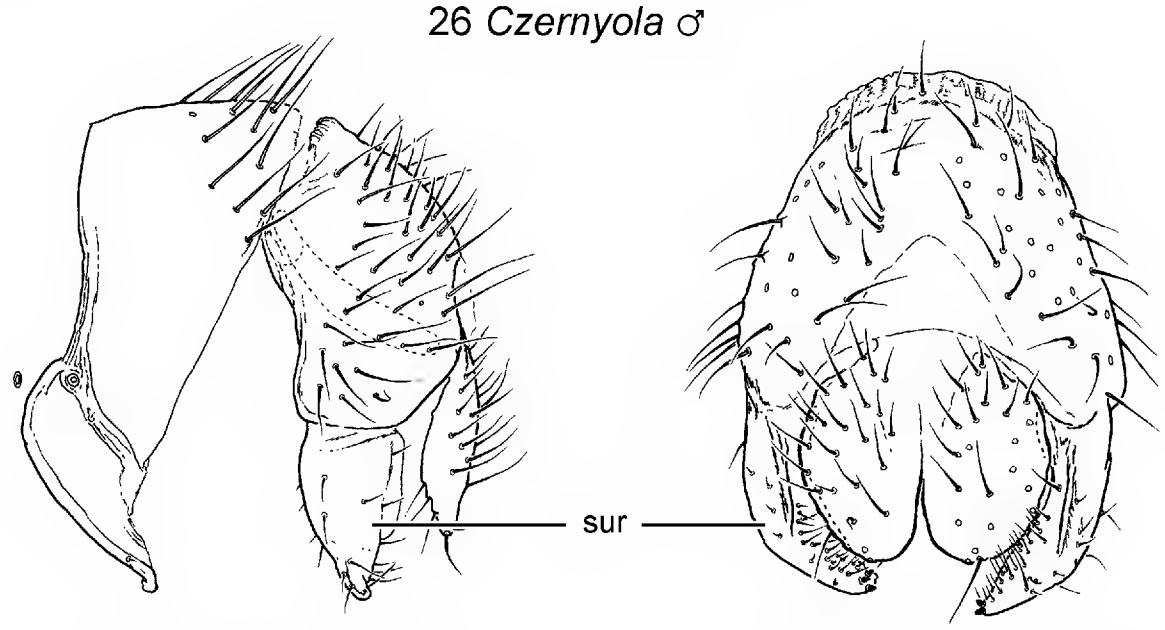
27 *Czernyola* ♂



25 *Czernyola* ♂



26 *Czernyola* ♂



28 *Czernyola* ♂ 29 *Czernyola* ♂

Figs 81.23–29. Male terminalia of Clusiidae: (23) external components of *Hendelia* sp., lateral view; (24) same, posterior view; (25) hypandrial complex of *Czernyola* sp., ventral view; (26) same, hypandrial complex, lateral view; (27) same, ejaculatory apodeme; (28) same, external components, lateral view; (29) same, external components, posterior view.

Abbreviations: cerc – cerci (fused); epand – epandrium; phapod – phallapodeme; hypd + pregt – hypandrium + pregonite; st – sternite; sur – surstylus.

Economic significance

No species of economic significance are currently known.

Classification

The Clusiidae has been treated as a representative of the superfamily Opomyzoidea (McAlpine 1989: 1458), or at least as a close relative of the Agromyzidae (Griffiths 1972: 213). A recent molecular study (Winkler *et al.* 2010) has revealed the superfamily to be an artificial grouping of families, however, and there is little substantial morphological evidence to establish any sister-group relationships with the Clusiidae (Lonsdale *et al.* 2010).

Within the Clusiidae, Frey (1960) first split the family into two subfamilies, with the Clusiinae defined by having one of the fronto-orbital setae inclinate (Fig. 2) and the Clusiodinae defined by having all of the fronto-orbitals reclinate (Fig. 4). Steyskal (1965: 805) later transferred *Czernyola* to the Clusiodinae (third posterior seta inclinate) (Fig. 3), leaving the subfamilies to be defined by having only the anterior fronto-orbital setae inclinate (Clusiinae) or reclinate (Clusiodinae). This system is still followed by Sasakawa (2011), although Lonsdale & Marshall (2006*a*) determined that neither of these subfamily concepts based on a single character of fronto-orbital chaetotaxy corresponded with clades based on other external morphological and terminalia characters. Based on a wider suite of characters, Lonsdale & Marshall (2006*a*) transferred *Heteromeringia* to the Clusiodinae and divided the Clusiinae into the new subfamily Sobarocephalinae and a reduced Clusiinae. These results were corroborated by the molecular analyses of Lonsdale *et al.* (2010), with the exception that the Chilean genus *Apiochaeta* Czerny was strongly supported as Sobarocephalinae. This resulted in a slightly refined classification that is more parsimonious biogeographically, with a mostly New World tropical Sobarocephalinae (some *Sobarocephala* are Nearctic or Old World tropical in distribution) and a mostly Old World tropical Clusiinae (although most *Clusia* are north temperate in distribution).

The genera of Clusiidae are now grouped as follows, with those occurring in the Afrotropics marked with an asterisk: 1) Sobarocephalinae – *Apiochaeta*, *Chaetoclusia* Coquillett, *Procerosoma* Lonsdale & Marshall and *Sobarocephala**. 2) Clusiinae – *Clusia*, *Melanoclusia* Lonsdale & Marshall, *Phylloclusia* Hendel and *Tetrameringia**. 3) Clusiodinae – *Allometopon**, *Clusiodes*, *Czernyola**, *Hendelia**, *Heteromeringia** and *Electroclusiodes* Hennig†.

The Sobarocephalinae consists of two small genera from the tropical Neotropics, the Chilean *Apiochaeta* and the largest genus of Clusiidae, *Sobarocephala*. *Sobarocephala* is mostly New World in distribution, but a number of species are found throughout the Old World tropics, mostly in the Oriental and Afrotropical Regions, but also in the eastern Palaearctic Region and parts of the Australasian Region as far south as northern Australia (Lonsdale 2014). Like the Clusiinae, this subfamily has an inclinate anterior fronto-orbital seta, but there are several derived male terminalia features (Figs 13–15) and a dorsal preapical seta is present on the mid tibia (absent in Clusiinae). The tibial seta is only absent in *Procerosoma*, which is typified by an overall reduction in chaetotaxy, but its sister-group relationship to *Sobarocephala* is strongly supported (Lonsdale & Marshall 2006*a*).

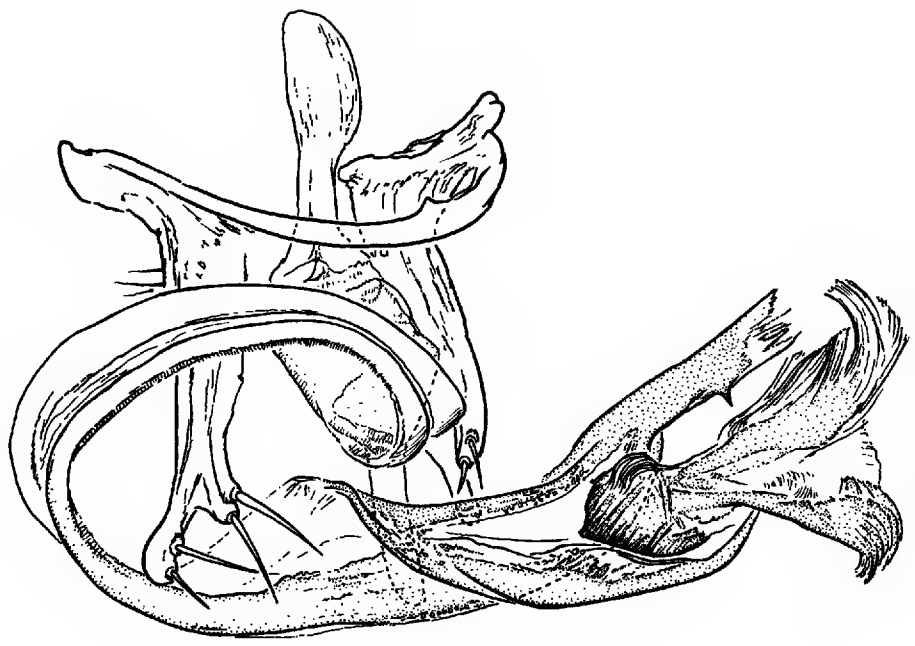
The Clusiinae are characterised by an absence of dorsal preapical setae on all tibiae, a slight posteromedial emargination on the frons and a small surstylus and paraphallus (Figs 16–19). There are also often minute black setulae on the frons, a relatively short distal section of vein M_1 and a strong horizontal fascia on the pleuron. Of the four clusiine genera, only *Tetrameringia* occurs in the Afrotropics, with species also found in Japan and eastern Australia. *Clusia* is north temperate and Oriental in distribution, *Melanoclusia* is restricted to Borneo (Lonsdale & Marshall 2008*a*) and *Phylloclusia* (the sister genus to *Tetrameringia*), is found from Sri Lanka to Borneo, Taiwan and Japan (Lonsdale & Marshall 2007*c*).

The Clusiodinae is a widespread and speciose subfamily with roots in the Oriental and Australasian Regions, and while most genera have entirely reclinate fronto-orbital setae, *Czernyola* has the third posterior seta inclinate (anterior 1 or 2 setae reclinate) (Fig. 3) and *Heteromeringia* (Fig. 2) has the anterior of its three fronto-orbital setae inclinate. Excluding *Allometopon*, the subfamily is further supported by numerous male and female terminalia characters (e.g., Lonsdale *et al.* 2010), as well as external characters, including a dorsally flattened and wrinkled scutellum and reduced extensions on the inner and outer margins of the pedicel. *Czernyola*, *Clusiodes* and *Hendelia* likely form a natural group, as these are the only Clusiidae with dorsal preapical setae on both the mid and hind tibiae; the last two are further supported as sister-taxa on the basis of numerous synapomorphies, including interfrontal setae and unique male terminalia (Lonsdale & Marshall 2007*b*). This subfamily is relatively well-represented in the Afrotropics by the widespread genera *Czernyola* and *Heteromeringia*, which appear to be the most frequently encountered taxa, *Hendelia* (Fig. 4), and the predominantly Australasian *Allometopon*, which occurs in Côte d'Ivoire, Madagascar and Seychelles.

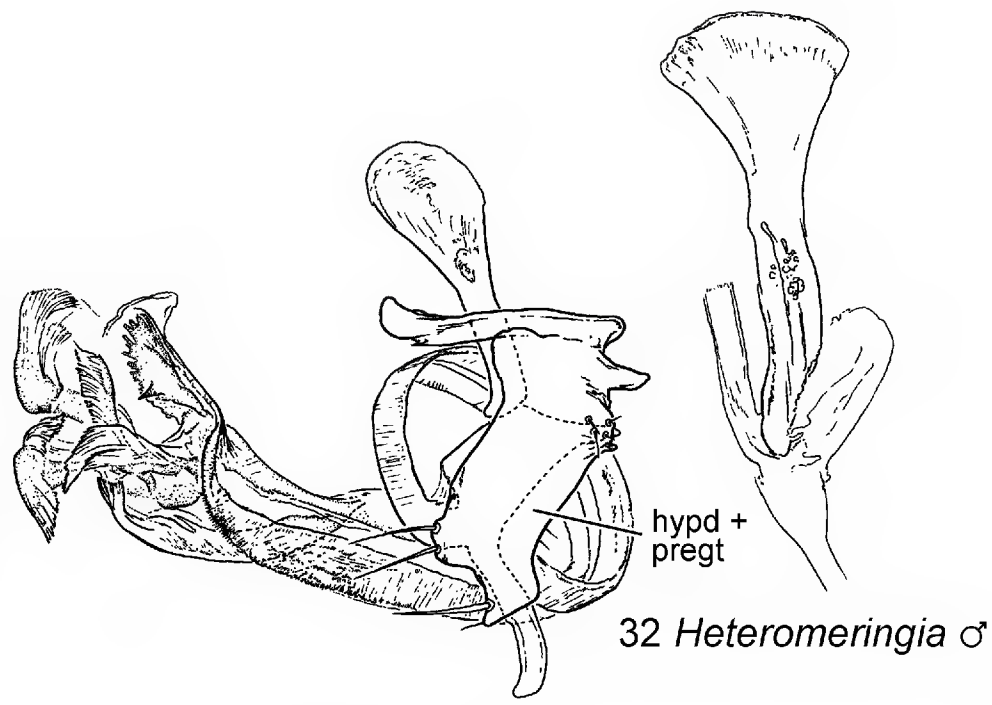
Identification

Due to a paucity of revisionary work on the Afrotropical Clusiidae, the fauna remains poorly known, although an identification key to the genera of sub-Saharan Africa was developed by Stuckenberg (1973), Lonsdale (2014) revised and keyed the Old World *Sobarocephala*, including nine Afrotropical species and Lonsdale (2016) similarly revised the world *Allometopon*, including five Afrotropical species. Lonsdale *et al.* (2010) published an identification key to the world genera of Clusiidae and Lonsdale *et al.* (2011) developed electronic keys to genera, both in dichotomous and matrix-based formats.

Descriptions of the Afrotropical fauna are found in Barraclough (2002), Lamb (1914), Lonsdale (2014), Stuckenberg (1973) and Verbeke (1968), including 16 species in four genera, although Barraclough (2002) is likely correct in estimating that there may be many more species to be discovered. The two species described by Verbeke (1968) were originally placed in *Strongylophthalmyia* Heller (not known from the Afrotropical Region), but these were recombined as *Heteromeringia* and *Tetrameringia* by Barraclough (2000). Clusiidae are best micro-pinned in the field for later double-mounting (see Chapter 2).



30 *Heteromeringia* ♂



31 *Heteromeringia* ♂

32 *Heteromeringia* ♂

33 *Heteromeringia* ♂

34 *Heteromeringia* ♂

Figs 81.30–34. Male terminalia of Clusiidae: (30) hypandrial complex of *Heteromeringia tephrinos* Lonsdale & Marshall, ventral view; (31) same, hypandrial complex, lateral view; (32) same, ejaculatory apodeme, lateral view; (33) same, external components, lateral view; (34) same, posterior view.

Abbreviation: hypd + pregt – hypandrium + pregonite.

Key to genera of Afrotropical Clusiidae

1. Frons with anterior fronto-orbital seta reclinate (*e.g.*, Figs 3, 4); if mid tibia with dorsal preapical seta, then hind tibia always with similar seta (CLUSIODINAE, excluding *Heteromeringia*) 2

– Frons with anterior fronto-orbital seta inclinate (*e.g.*, Fig. 2); if mid tibia with dorsal preapical seta, then hind tibia never with similar seta 4

2. Antenna with outer margin of pedicel with triangular extension long and sharply pointed (as in Fig. 6); head with posterior fronto-orbital seta as long, or longer than, other fronto-orbital setae; scutellum smooth and convex; preapical tibial seta absent; male terminalia with pregonite small and separate from hypandrium (as in Fig. 13); phallapodeme long, well-developed, with ventral shield; postgonite present; phallus rod-like, with basiphallus and distiphallus separate . . . . . *Allometopon* Kertész

– Antenna with outer margin of pedicel with triangular extension obtuse and blunt (*e.g.*, Fig. 5); head with posterior fronto-orbital seta often shorter than remaining fronto-orbital setae, or absent, leaving 2 setae (*e.g.*, Fig. 4); scutellum flat and longitudinally wrinkled; mid and hind tibiae with dorsal preapical setae; male terminalia with pregonite large and fused to hypandrium (*e.g.*, Figs 26, 31); phallapodeme greatly reduced; postgonite absent; phallus sac-like or atrophied, with basiphallus and distiphallus fused (epiphallus fused to basiphallus, or lost) 3

3. Head without interfrontal seta (Fig. 3); 4 or 5 pairs of fronto-orbital setae; third posterior seta inset and inclinate; genal setae small and setula-like, hind seta sometimes well-developed; male terminalia with surstylus without setae on outer face (at least anteriorly), usually directed ventrally and twisted so that inner face visible posteriorly (Figs 28, 29); phallapodeme rod-like (Fig. 26); ejaculatory apodeme mushroom-shaped (Fig. 27); female with ventral receptacle without subapical disc (Fig. 38). . . . . *Czernyola* Bezzi

– Head with interfrontal seta (Fig. 4); 2 or 3 fronto-orbital setae, all reclinate, with anterior and posterior setae small to absent; several medial genal setae more strongly developed; male terminalia with surstylus evenly setulose, usually small and medially directed (Figs 23, 24); phallapodeme carinate (Fig. 21); ejaculatory apodeme long and thin (Fig. 22); female with ventral receptacle with subapical disc. . . . . *Hendelia* Czerny

4. Lateral margin of antennal pedicel with triangular extension obtuse and blunt (Fig. 5); scutellum flat and longitudinally wrinkled; mid tibia without dorsal preapical seta; often with either white fore tarsomeres, or male with small pilose disc on anepisternum; male terminalia with distiphallus elongate, coiled, black and double-ribbed (Figs 30, 31); paraphallus absent; fused sternites 6–8 with enlarged ventral membranous pouch enclosing distiphallus when at rest; female with spermathecae strongly telescoped and dark; ventral receptacle with subterminal flagellum (Fig. 41) (CLUSIODINAE [in part]) . . . . . *Heteromeringia* Czerny

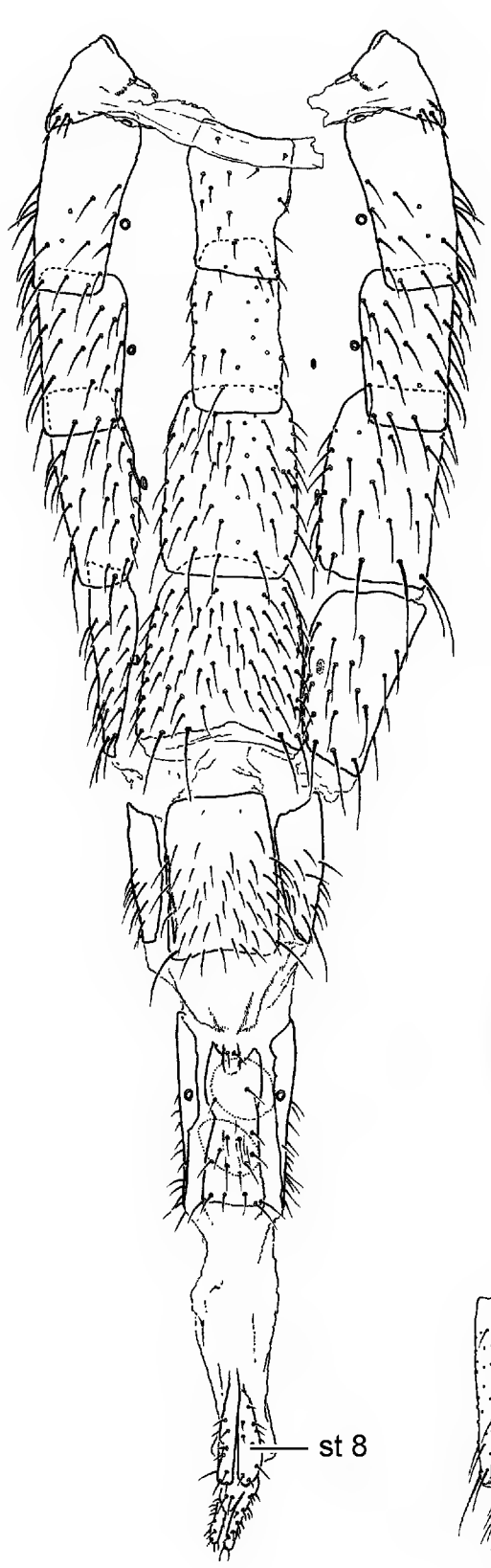
– Lateral margin of antennal pedicel with triangular extension long and sharply pointed (*e.g.*, Fig. 6); scutellum slightly convex and smooth; mid tibia sometimes with dorsal preapical seta; fore tarsomeres never white and male never with small pilose anepisternal disc; male terminalia with distiphallus composed of linear sclerite that is rod-like or with medial joint (*e.g.*, Figs 13, 16); paraphallus present; female with spermathecae not telescoped and usually clear; ventral receptacle without flagellum (*e.g.*, Fig. 36) 5

5. Head with 3 pairs of fronto-orbital setae; antennal arista with setulae dense at base; mid tibia with dorsal preapical seta; wing vein M_{1+2} ratio (length of ultimate section of vein M_1 divided by penultimate) of wing greater than 3.0 (Fig. 7); cell *bm* open; male terminalia with surstylus broadly rounded, without inner-basal process, although rarely with pointed extension on posterobasal margin (Figs 14, 15); distiphallus unbroken, relatively straight, with basal shield-like sclerite (Fig. 13) (SOBAROCEPHALINAE). . . . . *Sobarocephala* Czerny

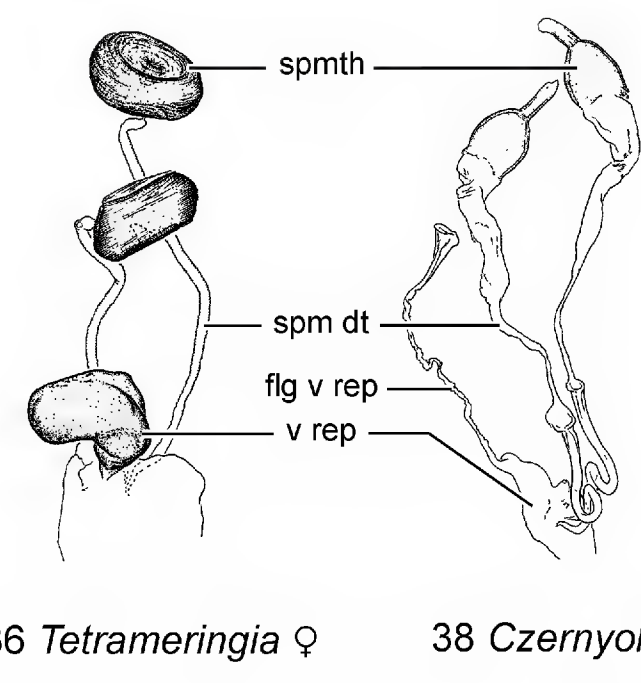
– Head with 4 pairs of fronto-orbital setae; antennal arista with setulae sparse along length; mid tibia never with dorsal preapical seta; wing vein M_{1+2} ratio of wing less than 2.7 (Fig. 8); cell *bm* closed; male terminalia with surstylus usually small to minute, triangular and/or with acute inner-basal process (Figs 18, 19); distiphallus elongate and broken medially, without ventrobasal shield-like sclerite (*i.e.*, exposed at base) (CLUSIINAE) . . . . . *Tetrameringia* McAlpine

Synopsis of the fauna

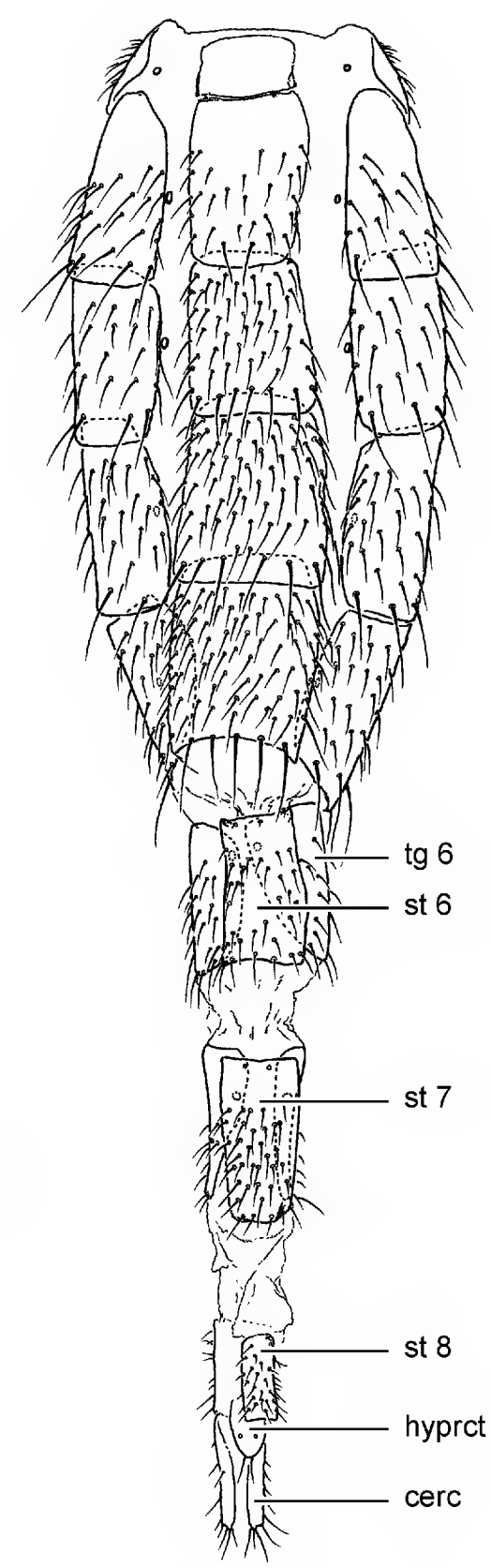
***Allometopon* Kertész** (Clusiodinae)**.** This infrequently encountered genus of 68 described species occurs primarily in the Australasian and Oriental Regions, but also Palaearctic Japan and some parts of the Afrotropics, although the fauna of the Afrotropics and South and South-east Asia will likely prove to be much more diverse following additional sampling. The genus was revised by Lonsdale (2016), who reported *A. flavum* Lamb, 1914 from Seychelles, *A. machaeroges* Lonsdale, 2016



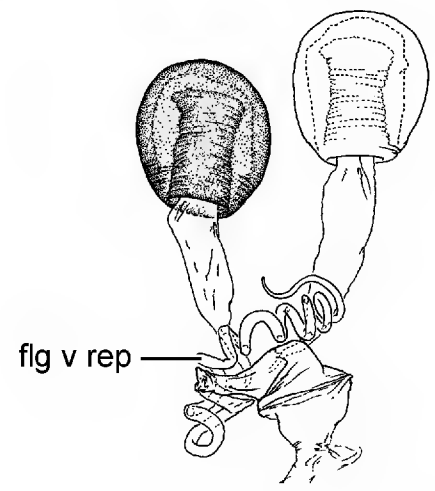
35 *Tetrameringia* ♀



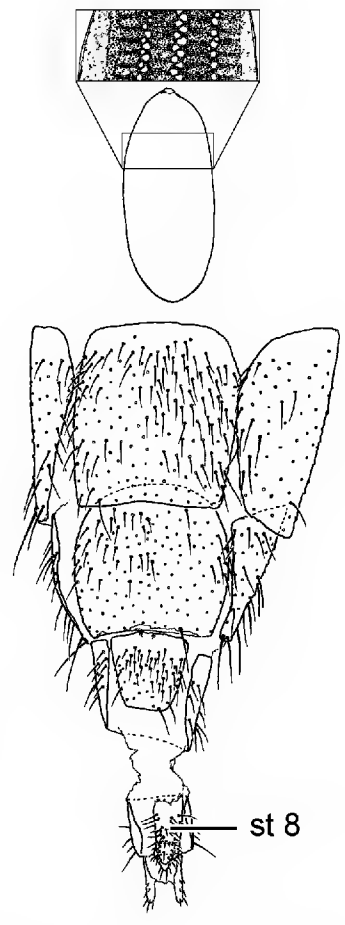
36 *Tetrameringia* ♀



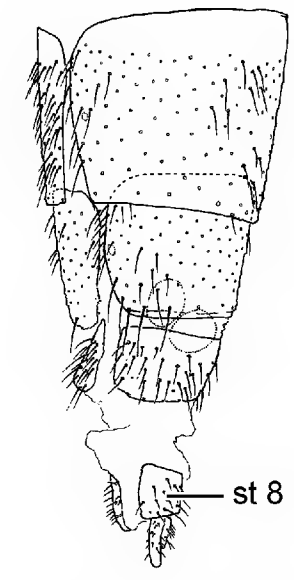
37 *Czernyola* ♀



38 *Czernyola* ♀



39 *Heteromeringia* ♀



40 *Heteromeringia* ♀

41 *Heteromeringia* ♀

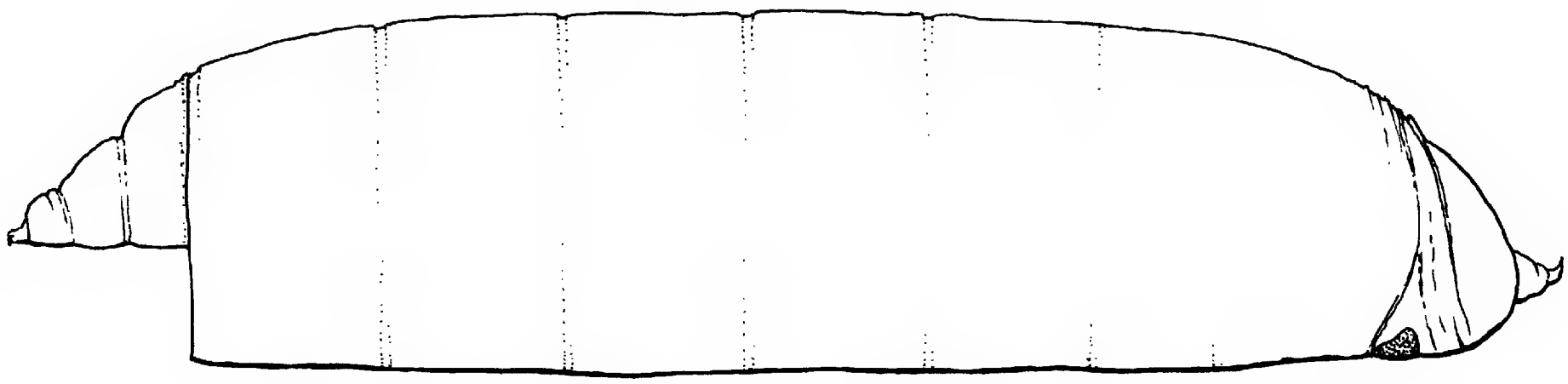
Figs 81.35–41. Female abdomen, egg and spermathecae of Clusiidae: (35) female abdomen of *Tetrameringia* sp., ventral view; (36) same, internal terminalia; (37) female abdomen of *Czernyola* sp., ventral view; (38) same, internal terminalia; (39) female abdomen beyond segment 4 of *Heteromeringia* sp., ventral view (egg and detail of egg micro-sculpture above); (40) same, abdomen beyond segment 4, lateral view; (41) same, internal terminalia.

Abbreviations: cerc – cercus; flg v rep – flagellum of ventral receptacle; hyprct – hypoproct; spm dt – sperm duct; spmth – spermatheca; st – sternite; tg – tergite; v rep – ventral receptacle.

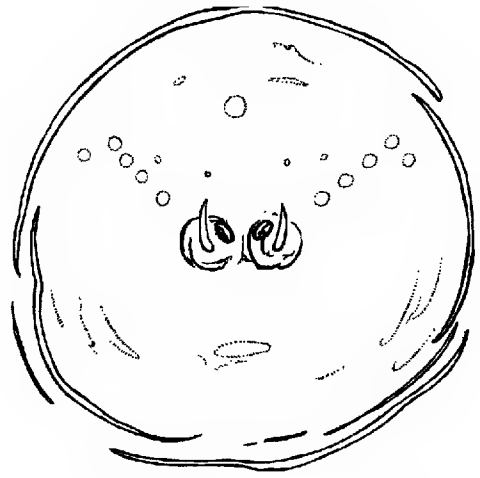
from Côte d'Ivoire and *A. fuscinum* Lonsdale, 2016, *A. glochis* Lonsdale, 2016 and one unnamed species only known from females from Madagascar. While species may be confused with *Sobarocephala*, which often has similar pale colouration, the anterior fronto-orbital seta of *Allometopon* is reclinate, there are no dorsal preapical tibial setae and the surstylus of the male terminalia is often larger and unusually shaped. All other clusiids with a reclinate anterior fronto-orbital seta (that is, the remainder of the subfamily, excluding *Heteromeringia*), have well-developed dorsal preapical setae on both the mid and hind tibiae. Most *Allometopon* are typically small, often being less than 4.0 mm in length, although the *A. palpale* species-group (South-east Asia and Sri Lanka) is unusually large and robust-bodied. Most species are also characterised by a large, triangular and silvery gena + postgena, a posteriorly displaced and reduced anterior dorsocentral seta and often an enlarged postpedicel. An identification key that includes Afrotropical species was provided by Lonsdale (2016).

***Czernyola* Bezzi** (Clusiodinae)**.** *Czernyola* – often treated as *Craspedochaeta* Czerny, 1903 in the literature – is a diverse genus mostly occurring in tropical regions, with several species extending into Nearctic and south temperate regions. There are 50 described species, but many unnamed taxa throughout the Old World tropics await revisionary treatment. The New World fauna is better known, with 31 described species (Lonsdale & Marshall 2006*b*). The genus is unknown in the Afrotropics, but a number of undescribed species have been examined, mostly from equatorial countries and it is expected to occur throughout much of sub-Saharan Africa. Species of *Czernyola* are generally small and dark, although the legs are often paler and some species are mostly yellow with a brown thoracic pattern. Males of Old World species are often paler than females and many of these exhibit a pronounced sexual dimorphism that is also characteristic of many Old World *Heteromeringia*, making species identification problematic. Most defining characters of the genus are male genitalic (Figs 25–29), but all species can be readily diagnosed in having reclinate fronto-orbitals with the third posterior seta proclinate and inclinate (Fig. 3). Furthermore, most Old World species, including all specimens examined from the Afrotropics, have the posterior fronto-orbital reduced, the posterior genal seta vibrissa-like and the spermatheca coiled.

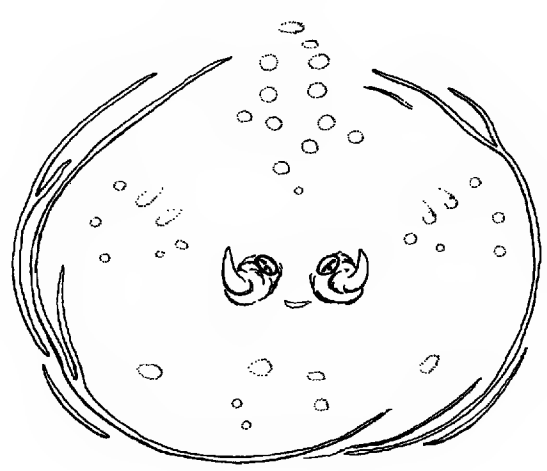
***Hendelia* Czerny** (Clusiodinae)**.** Most species of this morphologically diverse genus occur in tropical regions, with a minority in eastern Australia, but several are east Palaearctic in distribution and the type species (*H. beckeri* Czerny, 1903) is widespread from Japan to Europe. The genus was redefined by Lonsdale & Marshall (2007*b*) and it now includes 53 named species, many of which were previously treated as *Clusiodes,* its mostly north temperate sister genus. While *Hendelia* is defined



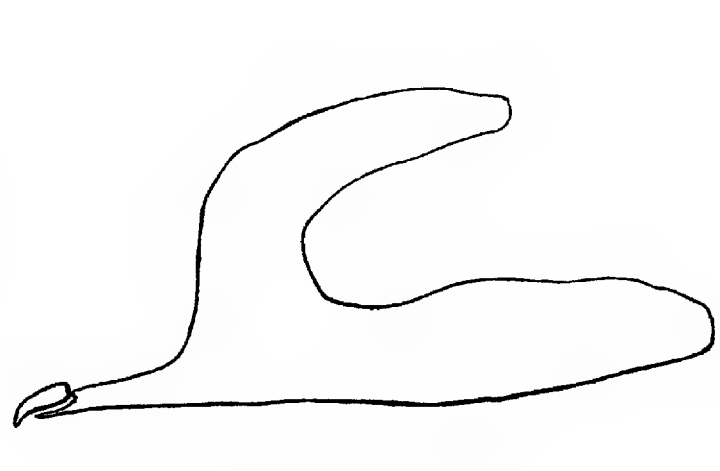
42 *Clusiodes*



43 *Clusiodes*



44 *Clusiodes*



45 *Clusia*

Figs 81.42–45. Immature stages of Clusiidae: (42) puparium of *Clusiodes johnsoni* Malloch, lateral view; (43) same, caudal view (non-Afrotropical); (44) same, *C. melanostomus* (Loew); (45) cephaloskeleton of third-instar larva of *Clusia flava* (Meigen), lateral view (non-Afrotropical). Figs 42–44 (Lonsdale & Marshall 2007*b*, figs 8–10); Fig. 45 (after Rotheray & Horsfield 2013, figs 59, 60).

on the basis of male terminalia characters (Figs 20–24), it can be easily identified on the basis of diagnostic external characters. Like *Clusiodes*, *Hendelia* has one pair of interfrontal setae and three reclinate fronto-orbital setae, with the anterior and posterior setae strongly reduced to absent (both are never absent simultaneously) (Fig. 4). Unlike *Clusiodes*, however, *Hendelia* lacks a pubescent arista, white notal fascia, or equidistant fronto-orbital setae if all three pairs are present. Furthermore, the male surstylus is almost invariably very small and medially directed and the head and/or antenna may be enlarged (Lonsdale & Marshall 2007*b*). Several undescribed species from equatorial countries are the only *Hendelia* known from the Afrotropics, but the genus is expected to occur throughout the region.

***Heteromeringia* Czerny** (Clusiodinae)**.** As is the case with *Czernyola* and *Hendelia*, species of *Heteromeringia* are mostly tropical in distribution with several outliers in the north temperate regions, but a considerable number of species are also found in Australia, predominantly in the east (Lonsdale 2009). Eighty-six species have been described, but dozens of unnamed species occur throughout the Old World tropics in the Afrotropical, Oceanian and Oriental Regions (Lonsdale, unpubl.). Only three species are currently described from the Afrotropics – *H. aethiopica* (Verbeke, 1968) (Democratic Republic of Congo), *H. nigriceps* Lamb, 1914 (Seychelles), and *H. tephrinos* Lonsdale & Marshall, 2007 (Seychelles, South Africa; replacement name for *H. nigrifrons* Lamb, 1914). *Heteromeringia*, redefined by Lonsdale & Marshall (2008*b*: 13), can be diagnosed by having an inclinate anterior fronto-orbital seta (similar to genera in the Clusiinae and Sobarocephalinae) (Figs 1, 2), a shallow angulate extension on the outer face of the pedicel (Fig. 5), no preapical tibial setae, minute to absent lateral scutellar setae and a long, coiled double-ribbed distiphallus (Figs 30, 31). Many Afrotropical species are also predominantly dark in colouration, with the legs and venter of the pleuron often being partly yellow and many males and some females have a small pilose macula on the anepisternum ("anepisternal disc"). *Heteromeringia* species are often associated with relatively open areas, such as tree falls and pastures and many species have been collected using dung, mushrooms or carrion (Lonsdale & Marshall (2010: 1048).

***Sobarocephala* Czerny** (Sobarocephalinae)**.** *Sobarocephala* is a large genus with 240 described species in the New World, most of which are found in tropical Central and South America. The Old World fauna was treated in Lonsdale (2014), (re) describing 29 species throughout the Oriental and Afrotropical Regions, as well as in parts of Oceania, northern Australia and the eastern Palaearctic. There are nine described Afrotropical species, including *S. plumicornis* (Lamb, 1914) (Seychelles), *S. milangensis* Stuckenberg, 1973 (south-east Africa) and *S. zuluensis* Stuckenberg, 1973 (South Africa) (Figs 13–15) and six species described by Lonsdale (2014): *S. doryphoros* (Madagascar, Seychelles), *S. insolata* (Madagascar), *S. laticrinis* (Tanzania), *S. magna* (Nigeria), *S. myllolabis* (Burundi) and *S. recava* (Madagascar). *Sobarocephala* can be differentiated from other Old World Clusiidae by having the anterior fronto-orbital seta inclinate, no interfrontal seta, a dorsal preapical tibial seta only on the mid leg and an open cell *bm* (Fig. 7). Species are mostly yellow, with variable brown patterning on the dorsum of the thorax and abdomen and many species have a short plumose arista with the branches more densely clustered basally. North temperate *Sobarocephala* are often found on fallen tree trunks, particularly those baited with dung, but tropical species (to date observed only in the New World), are also found around damp, mossy areas near water, usually on the underside of leaves (Lonsdale & Marshall (2010: 1043).

***Tetrameringia* McAlpine** (Clusiinae)**.** This is a relatively small genus with seven described species, but additional undescribed species are known from the Afrotropics. There is one described *Tetrameringia* from Japan, one from Laos, two from Australia and three from the Afrotropical Region, namely: *T. aethiopica* Stuckenberg, 1973 (South Africa), *T. distoma* (Verbeke, 1963) (Madagascar) and *T. stuckenbergi* Barraclough, 2002 (Malawi). The genus is defined by four fronto-orbital setae, the anterior of which is inclinate (although the posterior seta is sometimes reduced to absent in the Australian *T. ustulata* McAlpine, 1960). Male (Figs 16–19) and female (Figs 35, 36) terminalia strongly support *Tetrameringia* as the sister-group to *Phylloclusia*, known from South-east Asia and Sri Lanka (Lonsdale & Marshall 2007*c*). Australian *Tetrameringia* have been collected over a dry stream bed in dry forest (Lonsdale & Marshall 2007*c*).

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MARGINIDAE 82

(Margin Flies)

David A. Barraclough

Fig. 82.1. Male of *Margo* sp. (Madagascar) (photograph © S.A. Marshall).

Diagnosis

Small-sized (body length: 1.7–3.0 mm), glossy, mostly dark brown to black acalyptrate flies, with porrect antennae (flagellum prominent) (Fig. 1) and wing dark infuscated along costal margin to insertion of vein R_{2+3} or just beyond (Fig. 4).

Head (Figs 2, 3) with palpus and proboscis well-developed; each of 2 fronto-orbital setae reclinate, inserted on separate glossy orbital zone, not mesoclinate; postocellar setae absent; vibrissa weakly differentiated; antenna porrect, with subapical arista; arista with short vestiture.

Thorax without prothoracic precoxal bridge; 3 dorsocentral setae inserted well posterior to transverse suture; 1 postpronotal seta; 1 + 1 notopleural setae; 1 presutural seta; 1 supra-alar seta; 1 very long postalar seta (acrostichal and intra-alar setae absent); 2 scutellar setae, large subapical pair and smaller central pair slightly farther apart than subapicals; 1 relatively strong anepisternal seta; 1 strong posterior katepisternal seta (proepisternal and proepimeral setae absent). Wing (Fig. 4) with costal vein (*C*) unbroken, extended only to vein R_{4+5} or slightly beyond, with anterodorsal and anteroventral series of relatively long setulae, but no spine(s) differentiated; subcostal vein (*Sc*) incomplete, distally attenuated and merged with vein R_1 well before end of latter, or merging with costal vein below vein R_1 in dorsal view; vein R_1 distally very broad (trumpet-shaped); cells *bm* and *cua* complete or virtually so; vein *CuA+CuP* at most reaching about halfway to margin; vein A_1

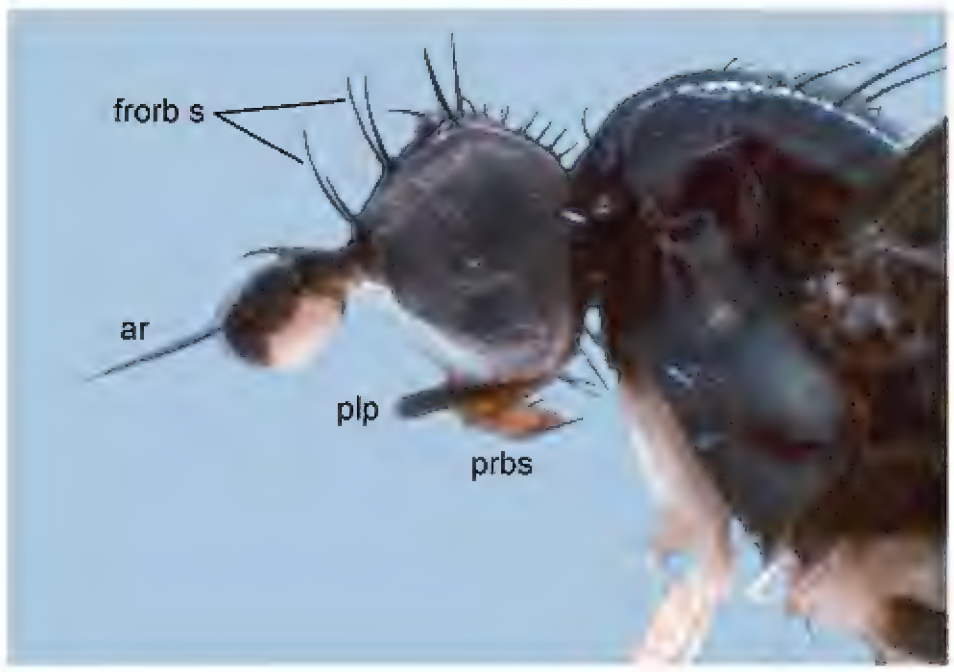
not visible beyond alula; alula large, without marginal fringe. Legs elongate; femora without strong setae; only mid tibia with differentiated preapical posterodorsal seta.

Abdomen with male postabdomen (Figs 5, 6) with tergite 6 and sternite 8 large; sternite 7 asymmetrically placed; surstylus freely moveable; hypandrium relatively simple, rather flat with thickened margins, forming ¾ circle connected posteriorly to anterior angles of epandrium (Fig. 6); phallus rigid beyond base; large clavate distiphallus with bulbous reflexed apex and slightly emarginate posterior lobe (Fig. 6); female abdomen without specialised elongate segments; cerci separate.

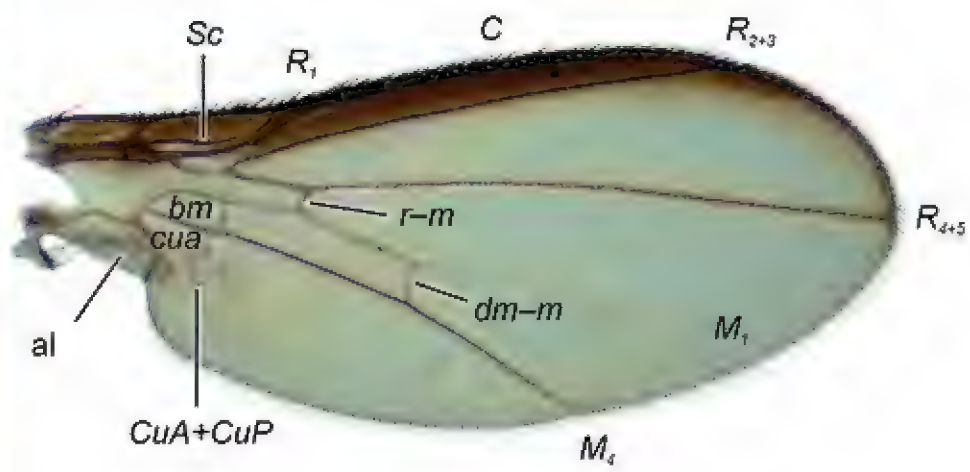
Marginidae are superficially most similar to some Clusiidae (see Chapter 81), but differ in having only 2 pairs of reclinate (never inclinate) fronto-orbital setae and costal breaks entirely absent.

Biology and immature stages

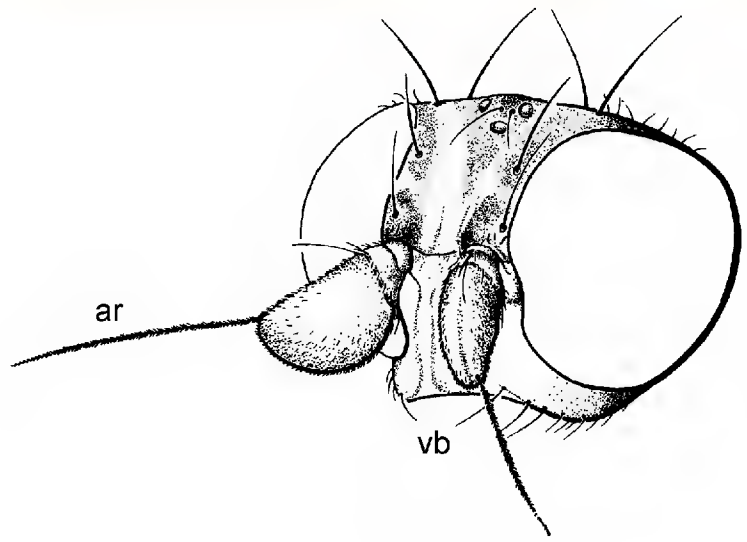
The Marginidae is one of the most poorly studied and understood Diptera families in the Afrotropical Region. The continental Afrotropical species *Margo aperta* McAlpine, 1991, has been collected only once (three specimens in 1955), from Chirinda Forest Reserve on the slopes of Mt Selinda in south-eastern Zimbabwe. The reserve comprises medium-elevation evergreen indigenous forest, at an elevation of 1,100–1,240 m (Hyde *et al*. 2013). The only published record of the family from Madagascar (the holotype), was along the mid-eastern coastal mountain belt and the family appears to be restricted there to the Evergreen Rainforest Biome, at elevations of 800–1,100 m (see below). The immature stages are undescribed and no fossils are known in the family.



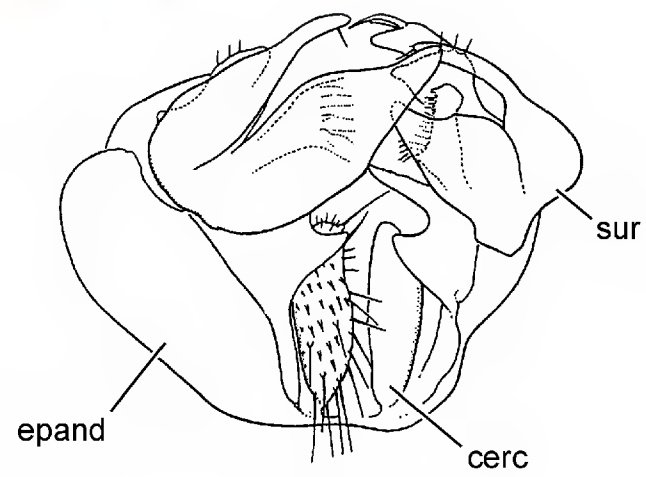
2 *Margo*



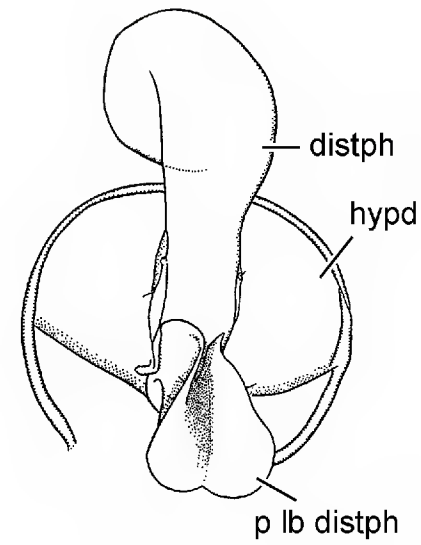
4 *Margo*



3 *Margo*



5 *Margo* ♂



6 *Margo* ♂

Figs 82.2–6. Head, wing and male terminalia of Marginidae: (2) head and thorax of *Margo* sp., lateral view; (3) same, *M. aperta* McAlpine, oblique view; (4) wing of *Margo* sp., dorsal view; (5) male terminalia of *M. aperta*, terminal oblique view; (6) same, male hypandrium, with ventral view of phallus and distiphallus. Fig. 3 (Barraclough 1995, fig. 28), Figs 5, 6 (McAlpine 1991, figs 6, 5, respectively).

Abbreviations: al – alula; ar – arista; *bm* – basal medial cell; *C* – costal vein; cerc – cercus; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; distph – distiphallus; *dm–m* – discal medial crossvein; epand – epandrium; frorb s – fronto-orbital setae; hypd – hypandrium; M_1 – first branch of media; M_4 – fourth branch of media; p lb distph – posterior lobe of distiphallus; plp – palpus; prbs – proboscis; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Sc* – subcostal vein; sur – surstylus; vb – vibrissa.

Economic significance

Marginidae have no known economic significance.

Classification

The family has been little studied since its description. McAlpine (1991) provisionally placed the Marginidae in the superfamily Opomyzoidea, due to variable degrees of resemblance to several opomyzoid families and due to a lack of significant resemblance to other schizophoran superfamilies of Diptera. Amnon Freidberg (pers. comm. 2013), however, supplied recently collected Madagascan material to the Tree of Life Project and the results of this molecular analysis support placement of the family as sister-group to the non-Afrotropical Nannodastiidae + Canacidae (Wiegemann *et al*. 2011), in a probably paraphyletic Opomyzoidea (Pape *et al*. 2011).

Identification

Barraclough (1995) identified the family Marginidae in an identification key to all Southern African families of acalyptrate Diptera. Species of the genus are readily distinguished using colour characters. Furthermore, the continental Afrotropical and type species (*Margo aperta*) is immediately recognised in lacking crossvein *dm–m* (present in the single Madagascan species). McAlpine's (1991) paper provides a comprehensive generic description. Marginidae are best micro-pinned in the field for later double-mounting (see Chapter 2).

Synopsis of the fauna

***Margo* McAlpine.** An endemic genus of two described species, *M. aperta* described from Zimbabwe and *M. clausa* McAlpine, 1991, described from Madagascar. The monogeneric family Marginidae is likely restricted to the south-eastern part of the Afrotropical Region. Recent investigations have revealed the presence of more than 10 specimens of both sexes from an additional four localities in eastern Madagascar; one of these localities being in the far north. It is probable that this material includes at least one undescribed species. Further sampling in Afromontane forest in Malawi, Mozambique and Zimbabwe may reveal additional material. An identification key to the two described species was provided by McAlpine (1991).

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ODINIIDAE 83

(Odiniid Flies)

Stephen D. Gaimari

Fig. 83.1. Female of *Odinia surumuana* Prado (non-Afrotropical) (photograph © S.A. Marshall).

Diagnosis

Small- to moderately large-sized (body length: 2.5–6.0 mm), compact-bodied, strongly bristled acalyptrate flies (Figs 1–15); pruinose silvery to dull grey and variously mottled or marked with brownish (Figs 6–13), or vittate (Fig. 15), sometimes with black velvety patches (Fig. 2), or sometimes predominantly brownish (Fig. 4).

Head higher than long (Figs 30–33); vertical setae long and strong, inner seta very long (Fig. 30); postocellar setae divergent, usually well-developed (Fig. 15); ocellar plate normal (Figs 17, 19, 21), to unusually prominent as an ocellar tubercle (most Traginopinae) (Figs 22, 31, 33); ocellar setae well-developed, proclinate (Figs 2, 3, 24); with 3 or more pairs of fronto-orbital setae, posterior 2 reclinate (rarely 1, with second absent), anterior 1–5 (usually 1) inclinate (Fig. 25); frons and face in line or sloping (Traginopinae) (Figs 31–33) to distinctly angulate (most Odiniinae) (Fig. 30); lunule bare or with few setulae, narrowly exposed (Figs 20, 24), or broadly exposed (Figs 18, 26), sometimes with dorsomedial black pruinose macula; gena broad (Figs 30–33), often with upturned genal seta (Figs 31, 33); vibrissa strong (Figs 25, 27, 29); antennal scape very short; pedicel notched anterodorsally, with strong seta; postpedicel *ca* as high as long, rounded at apex (Fig. 27), sometimes large (Fig. 21); arista bare (Figs 17, 21, 27) to plumose (Figs 29, 33).

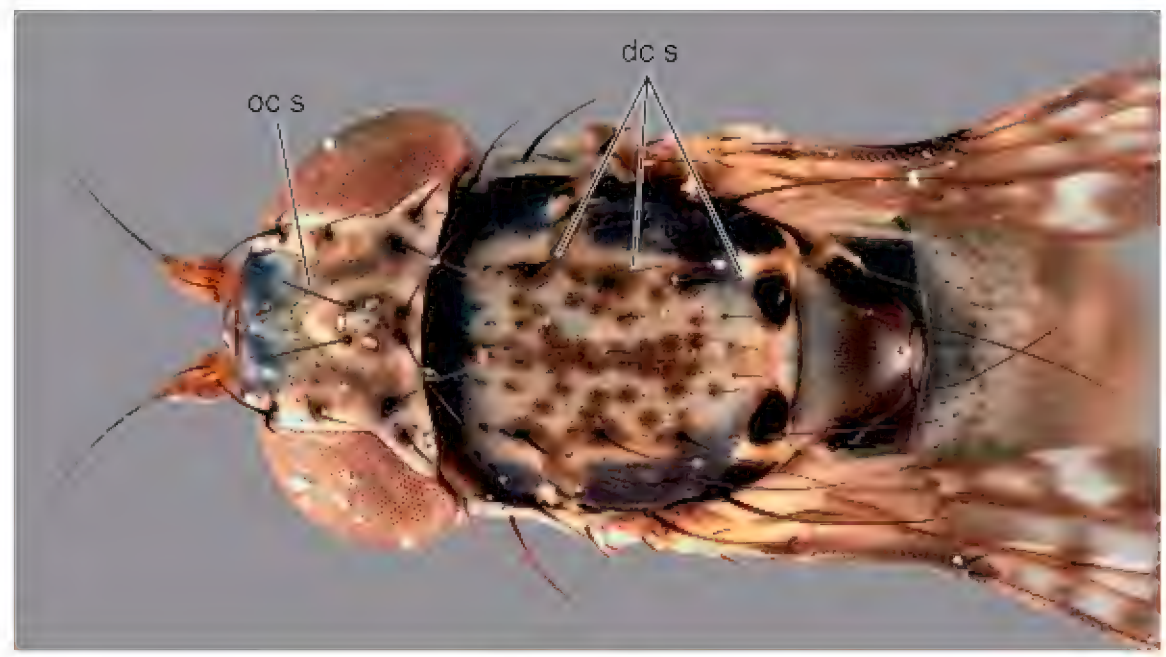
Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2021. Manual of Afrotropical Diptera. Volume 3. Brachycera—Cyclorrhapha, excluding Calyptratae. *Suricata* 8. South African National Biodiversity Institute, Pretoria; pp. 1885–1901.

Thorax with mesonotum with 3–5 dorsocentral setae, 0–1 (occasionally 2) presutural and 3 (Figs 11, 13) or 4 (Fig. 15) postsutural; 1 (Fig. 36) or 3 (Fig. 35) postpronotal setae; 1 to several postsutural intra-alar setae; 1 presutural and 1 postsutural supra-alar setae; 2 postalar setae; 2 notopleural setae; prescutellar acrostichal seta present, rarely absent or reduced; additional acrostichal setae in row (Fig. 7) or absent (Figs 11, 13), with setulae only; prescutellum present (Fig. 11) or absent (Fig. 13); scutellum with 2 pairs of marginal setae, scutellar disc bare (Fig. 37) or setulose (Fig. 38), sometimes sparsely (Fig. 39); anepisternum bare (Figs 34–36) or with posterior marginal setae; katepisternum with 2 (Fig. 34), 3 (Figs 35, 36) or 4 large setae along dorsal margin; upper proepisternum in front of anterior spiracle bare (Figs 34–36); proepisternal seta present (Fig. 36); prosternum free, bare. Wing membrane usually with pattern, from simple darkened crossveins (Figs 45, 46), to complexly pictured or mottled (Figs 40, 42–44), occasionally unmarked (Fig. 41); costal vein (*C*) extending to vein R_{4+5} (Figs 40–42, 44, 45) or to M_1 (Figs 43, 46), with subcostal break only (Fig. 46); subcostal vein (*Sc*) incomplete (Fig. 46); crossvein *dm–m* present (Figs 42, 43, 45, 46) or absent (Figs 40, 41, 44). Legs stout; femora often enlarged (especially hind femur of males); often with tibial fasciae (Figs 6, 8); preapical dorsal tibial setae present on one or more legs.

Abdomen relatively short, broad, usually patterned with grey and/or brown pruinescence (Figs 47, 49), sometimes extensively (Fig. 48) or entirely brown (Fig. 50) brown; male terminalia with epandrium setose (Figs 51, 54); surstylus present (Figs 54, 55) or absent (Fig. 51), or sometimes divided into inner and outer surstyli (Figs 54, 55); hypandrium broad (Figs 56, 57) or narrow (Figs 52, 53); phallapodeme elongated (Figs 52, 53, 56, 57); ejaculatory apodeme absent.

Egg and the first- and second-instar larvae unknown. Third-instar larvae of typical schizophoran type; body essentially bare, except for small fringe of setulae anterior to oral opening (Fig. 60) and paired creeping welts anteroventrally on abdominal segments 2–7 (Fig. 58); each welt consisting of pad of large spines anteriorly and posteriorly directed, surrounded by similarly directed smaller spines (spines likely allow larva to grip and anchor themselves against smoothly bored tunnel walls;

2 *Afrodinia* ♂



3 *Afrodinia* ♂

4 *Coganodinia* ♀

5 *Coganodinia* ♀

Figs 83.2–5. Habitus and heads and thoraces of Odiniidae: (2) habitus of *Afrodinia* sp., lateral view ♂; (3) same, head and thorax, dorsal view; (4) habitus of *Coganodinia cornesi* (Cogan), lateral view ♀; (5) same, head and thorax, dorsal view. Figs 4, 5 (photographs © Trustees of the Natural History Museum, London).

Abbreviations: dc s – dorsocentral setae; oc s – ocellar seta.

Kirk-Spriggs & Barraclough 2009); caudal segment bearing paired fleshy lobes (expansion likely aids locomotion; Lewis 1979), near bilobed perianal pad; prothoracic spiracles (Figs 58, 59), inserted dorsolaterally (not as dorsal as in related Agromyzidae), each with 4–12 papillae, arranged in marginal rosette around expanded apex on short stalk (Fig. 59); posterior spiracles small, each with 3 diverging oval spiracular openings distally on tubular extension set on dome-shaped protuberance; paired protuberances separated distally, but fused basally; cephaloskeleton (Fig. 60) similar to other acalyptrate larvae, with separate intermediate and basal sclerites, long parastomal bar, dental sclerite; intermediate sclerite subdivided (in *Turanodinia* Stackelberg), or entire (in *Afrodinia* Cogan and other genera); occasionally (in *Traginops* Coquillett) with an additional small sclerite between the dental and intermediate sclerites; mouthooks simple, curved; basal sclerite with ventral cornu larger than dorsal cornu.

Puparium barrel-shaped, tapered both anteriorly and posteriorly; features described largely as for third-instar (as described above). Puparium of Afrotropical species of *Afrodinia* thoroughly treated by Kirk-Spriggs & Barraclough (2009), with description and SEM figures; puparium of *Afrodinia* possesses respiratory horn at lateral margin of abdominal segment 1, retracted into opening, common at least in genus *Odinia* Robineau-Desvoidy, but different in *Neoalticomerus* Hendel and *Traginops*; puparium of *Afrodinia* with 6 papillae on each prothoracic spiracle.

Of the families with three or more fronto-orbital setae, only a few are even superficially similar to odiniids and few specifically have two posterior reclinate fronto-orbital setae and one (to several) anterior inclinate fronto-orbital setae. Most Agromyzidae (see Chapter 86) lack preapical dorsal tibial setae, have slender legs, only rarely have patterned wings and sometimes have a more elongated, tapered abdomen (in females distinctly specialised for piercing plant tissue with a sclerotised oviscape). Of particular note is the New World genus *Paraneossos* Wheeler (Heleomyzidae), which is superficially similar to *Odinia*, with three fronto-orbital setae, identical head shape, overall body form and colouration; however, the species of this genus are small (1–2 mm), the anterior fronto-orbital seta is reclinate,

6 *Odinia* ♀

7 *Odinia* ♀

8 *Traginops* ♀

9 *Traginops* ♀

Figs 83.6–9. Habitus and heads and thoraces of Odiniidae: (6) habitus of *Odinia* sp., lateral view ♀; (7) same, head and thorax, dorsal view; (8) habitus of *Traginops* sp., lateral view ♀; (9) same, head and thorax, dorsal view.

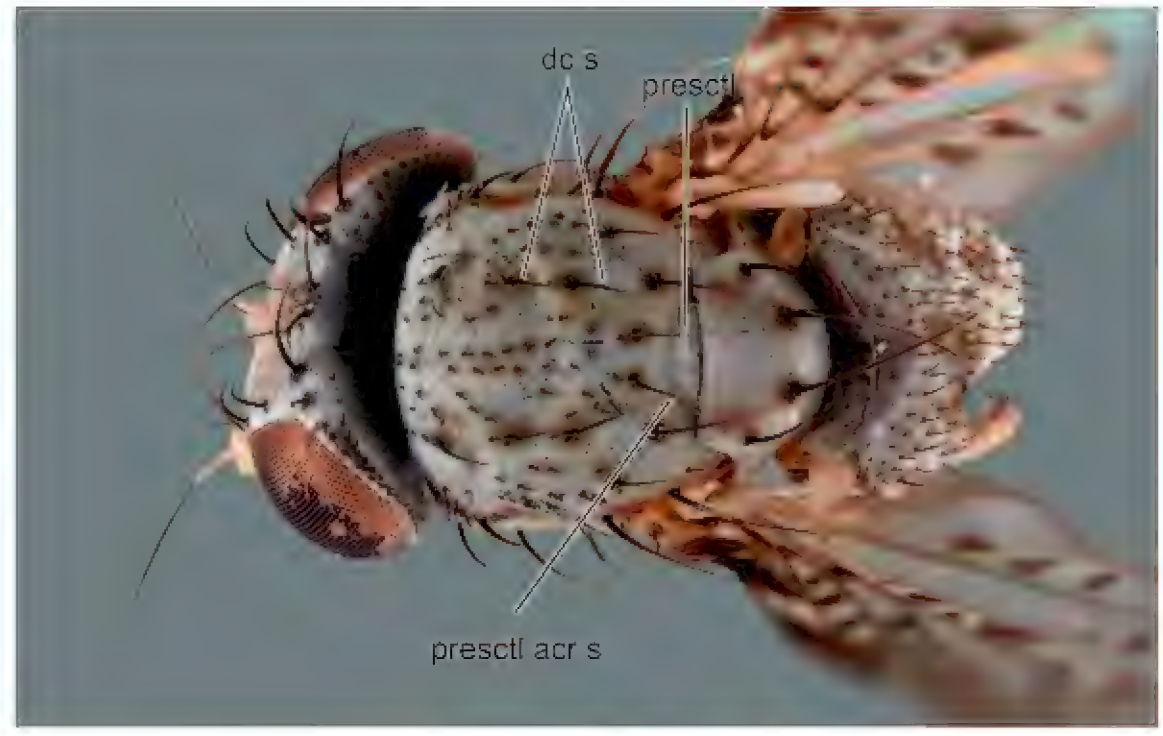
Abbreviations: acr s – acrostichal setae; dc s – dorsocentral setae; tb – tibia.

the postocellar setae are convergent to parallel and the costal vein (*C*) is weakly spinose. Other families, such as Anthomyzidae (see Chapter 87), Clusiidae (see Chapter 81) and non-Afrotropical Acartophthalmidae, are also distinctly more slender-bodied. Clusiids sometimes have the same typical fronto-orbital setal arrangement as odiniids (two reclinate posterior, one inclinate anterior), but the setae are much thinner and more delicate, as is the case for all setae on the head and thorax; the gena is narrow; the antennal pedicel often has a characteristic triangular extension laterally; the postpedicel often bears the arista terminally to subterminally; the subcostal vein (*Sc*) is complete; and the abdomen is slender. In acartophthalmids, the fronto-orbital setae are all lateroreclinate and the scutum lacks a presutural dorsocentral seta. In Anthomyzidae, the fronto-orbital setae are all reclinate, with the anterior seta weak, the postocellar setae are convergent if present and the scutum lacks a presutural dorsocentral seta. Other families that can superficially resemble odiniids in colouration and habitus, such as Chamaemyiidae (see Chapter 76) (some odiniids even share the characteristic prescutellum, which is an unusual state) and Lauxaniidae (see Chapter 74), are easily differentiated by their lack of vibrissae, unbroken costal vein (*C*), convergent postocellar setae and having, at most, two fronto-orbital setae. Others include some Drosophilidae (see Chapter 106), such as *Phortica* Schiner, with similar colouration, but are easily differentitated by the condition of the fronto-orbital setae, with two pairs reclinate and the anterior one to several inclinate.

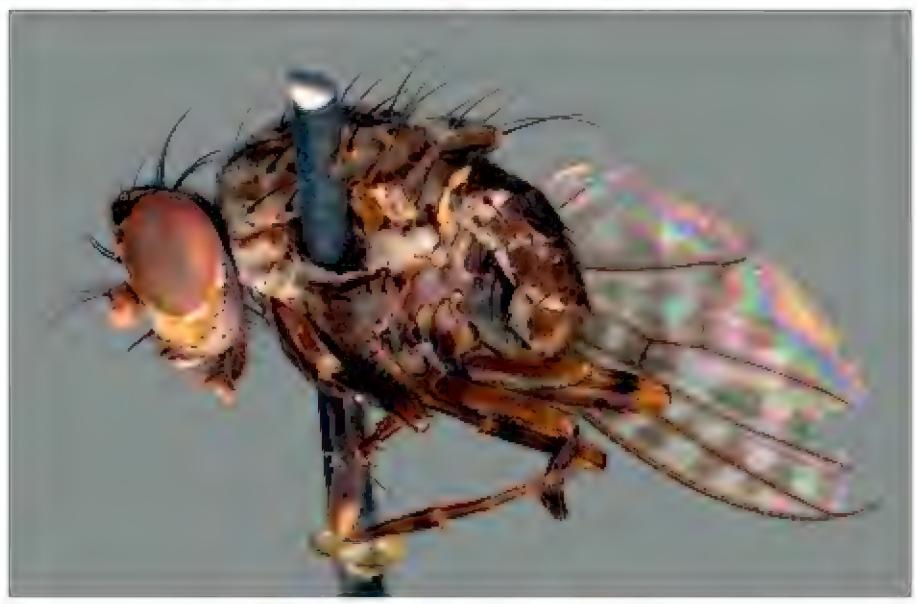
Biology and immature stages

Few studies describe the biology of species of Odiniidae, with the most current summary published by Gaimari & Mathis

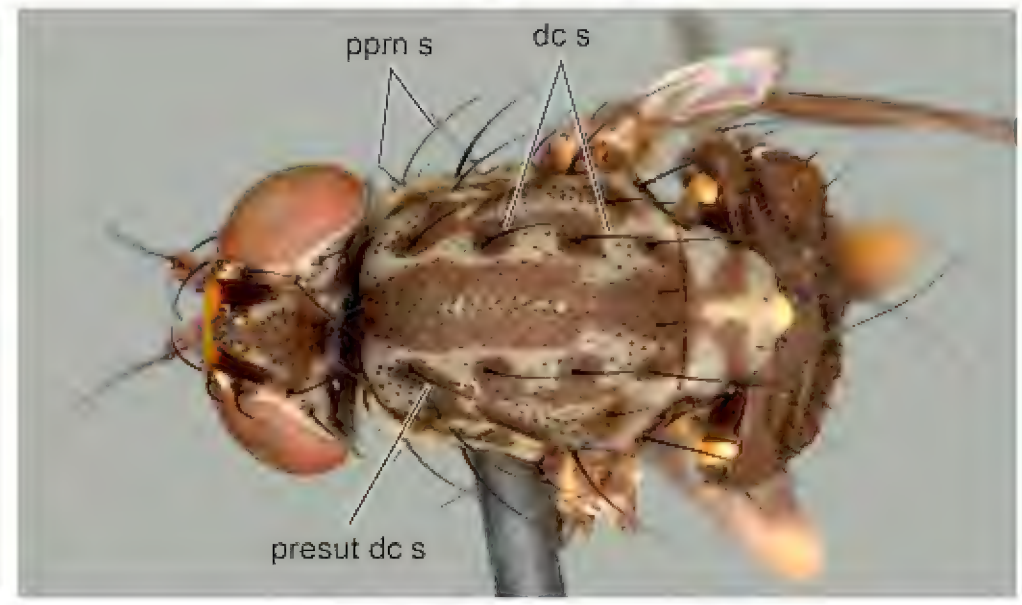
10 Undescribed genus A ♀



11 Undescribed genus A ♀



12 Undescribed genus C ♂



13 Undescribed genus C ♂

Figs 83.10–13. Habitus and heads and thoraces of Odiniidae: (10) habitus of Undescribed genus A, lateral view ♀; (11) same, head and thorax, dorsal view; (12) habitus of Undescribed genus C (*Paratraginops ruwenzoricus* Cogan), lateral view ♂; (13) same, head and thorax, dorsal view. Figs 12, 13 (photographs © Trustees of the Natural History Museum, London).

Abbreviations: dc s – dorsocentral setae; fr – frons; pprn s – postpronotal setae; presctl – prescutellum; presctl acr s – prescutellar acrostichal seta; presut dc s – presutural dorsocentral seta.

(2011). Odiniids are most commonly found in forested ecosystems, where their biological activities occur. Specimens are most commonly collected in Malaise traps or associated with tree trunks, sap flows or beetle galleries. Some species are known to feed on polypore fungi on trees (Máca *et al*. 2005: 283; MacGowan & Rotheray 2002), or are attracted to bracket fungi as adults (Chandler 2010: 421). Krivosheina (2006) observed their constant presence around bark beetles and the dipteran families Bibionidae and non-Afrotropical families Hesperinidae and Pachyneuridae. Some species of *Odinia* have been collected in McPhail traps baited with vinegar (Carles-Tolrá 1996), or various yeast mixtures (Sabrosky 1959; Steyskal 1963). Interestingly, odiniids have been found to be abundant in forest canopies (Barkeley 2009; Stork 1991; Tschirnhaus 2008), including canopies of *Senegalia* and *Vachellia* (as *Acacia*) (Fabaceae) in Tanzania (Krüger & McGavin 1998).

Although few species have known biologies, those with known larvae or puparia are associated with trees, such as those that attract the adults. Usually, they are associated with galleries of wood-boring beetles, with several life history possibilities from saprophagy to predation. Of particular interest here, Kirk-Spriggs & Barraclough (2009) discussed an Afrotropical species of *Afrodinia* (nr. *medleri* Cogan) reared from "gum" in tunnels of *Vachellia karroo* (Hayne) Banfi & Galasso (Fabaceae) in South Africa. The specimens studied by them were previously discussed by Bearder & Martin (1980), who deduced that the liquid gum accumulated during and after occupation by beetle and moth larvae provide an excellent medium for the *Afrodinia* larvae and that the fly may further stimulate gum production. An interesting note is that they may be eaten by the Mohol bushbaby, *Galago moholi* Smith (Primates: Galagidae).

Among extralimital species, relevant examples of rearing records from beetle tunnels include weevils (Curculionidae in the subfamilies Cryptorhynchinae (Krivosheina 1981: 145; Shewell 1960), Platypodinae (Sabrosky 1959) and Scolytinae (Lewis 1979; Zubkov & Kovalev 1975), as well as the coleopterous families Buprestidae (Sabrosky 1959), Cerambycidae (Grimble & Knight 1970, 1971; Grimble *et al*. 1971; Krivosheina & Krivosheina 1996; Yang 1984), Oedemeridae (Collin 1952) and Tenebrionidae (Sabrosky 1959).

14 Undescribed genus B ♀ 15 Undescribed genus B ♀

Figs 83.14–15. Habitus and heads and thoraces of Odiniidae: (14) habitus of Undescribed genus B (*Odinia connecta* Cogan), lateral view ♀; (15) same, dorsal view. Figs 14, 15 (photographs © Trustees of the Natural History Museum, London).

Abbreviations: dc s – dorsocentral setae; dc vit – dorsocentral vitta; poc s – postocellar setae; presctl – prescutellum.

As interesting non-beetle exceptions, several species are known as associates and possibly predators, of lepidopteran caterpillars in enclosed spaces, such as tunnels of Cossidae (Campadelli 1995; Krivosheina 2006), Gelechiidae (Kato 1952), Sesiidae (Pakalniškis & Podénas 1992: 74) and Tortricidae (Steyskal 1963) and galls of Aegeridae (Beschovski & Georgiev 1993). Krivosheina (1981: 154) reported that several Palaearctic species attack larvae of certain wood-infesting Diptera. One Asian species was reared from egg masses of mealybugs (Stackelberg 1944), which may appear odd as a life history for an odiniid, but is perfectly reasonable, as the microcosm associated with the mealybug egg masses can be quite diverse, with many different organisms involved (from mites to predaceous fly larvae, to saprophagous moth larvae, many beetles, *etc.*) and the dense honeydew secreted by the mealybugs has intensive fungal growth. Ultimately, larvae of this species could be associated with this sub-bark micro-habitat in a variety of ways, from consuming fungi, to insect frass, to predation. Other species are known from sap fluxes on deciduous trees (Krivosheina & Krivosheina 1996; Papp 1995).

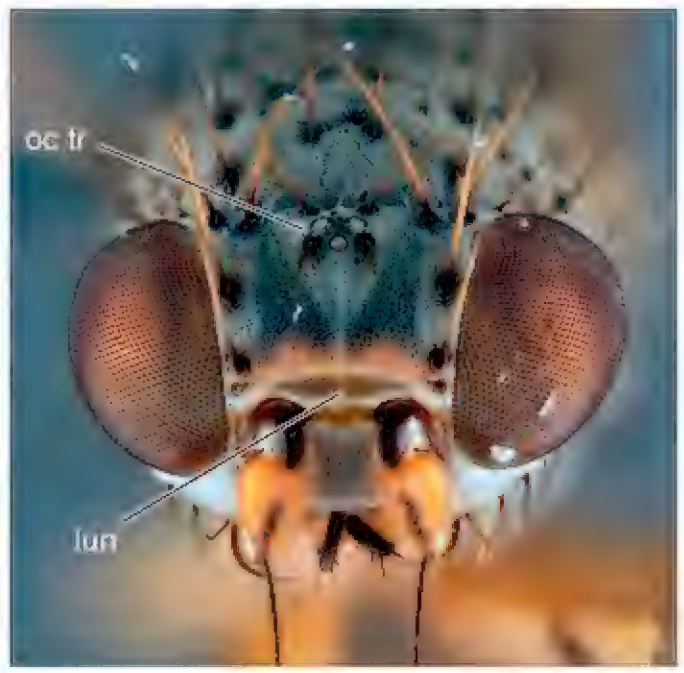
Specific life history data are lacking in this family, with some exceptions. Yang (1984) and Pulkkinen & Yang (1984) provided details of the natural history of a Holarctic species of *Odinia*, finding that oviposition of 15–20 eggs occurred at the entrance to a cerambycid beetle tunnel, with larvae then devouring the beetle frass, crawling towards the beetle's pupal chamber, which they then attacked externally or bored internally, also displaying cannibalism. Full development of the odiniids did not depend on devouring the beetle pupa and they occasionally did not even attack the pupa. For the Afrotropical species of *Afrodinia* discussed by Kirk-Spriggs & Barraclough (2009), the larvae took 39–46 days to develop before pupariation, which may indicate the food source is nutritionally poor and adults eclosed 17–22 days after pupariation.

16 *Afrodinia* ♂

17 *Afrodinia* ♂

18 *Coganodinia* ♀

19 *Coganodinia* ♀



20 *Odinia* ♀

21 *Odinia* ♀

Figs 83.16–21. Heads of Odiniidae: (16) *Afrodinia* sp., frontal view ♂; (17) same, lateral oblique view; (18) *Coganodinia cornesi* (Cogan), frontal view ♀; (19) same, lateral oblique view; (20) *Odinia* sp., frontal view ♀; (21) same, lateral oblique view. Figs 18, 19 (photographs © Trustees of the Natural History Museum, London).

Abbreviations: a frorb s – anterior fronto-orbital seta; ar – arista; lun – lunule; oc tr – ocellar triangle; pped – postpedicel.

Mature larvae or puparia have been described for 13 species (only one of which is Afrotropical) in five genera (three of which have Afrotropical species). For the Afrotropical species, a detailed stereoscan microscopy study of the puparium of a species of *Afrodinia* was undertaken by Kirk-Spriggs & Barraclough (2009), along with a review of the species of the family with known, or partially known, immature stages and biologies. For genera found in the Afrotropical Region, immature stages are at least partially known for *Odinia* (Kato 1952; Lewis 1979; Krivosheina 1981: 152; Yang 1984; Zubkov & Kovalev 1975) and *Traginops* (Shewell 1960) and the extralimital genera include *Turanodinia* (Krivosheina & Krivosheina 1996; Papp 1995) and *Neoalticomerus* (Shewell 1960). Ferrar (1987: 256, 741), Foote (1991: 818), McAlpine (1987: 864) and Smith (1989) also provided useful figures and general discussion of immature stages.

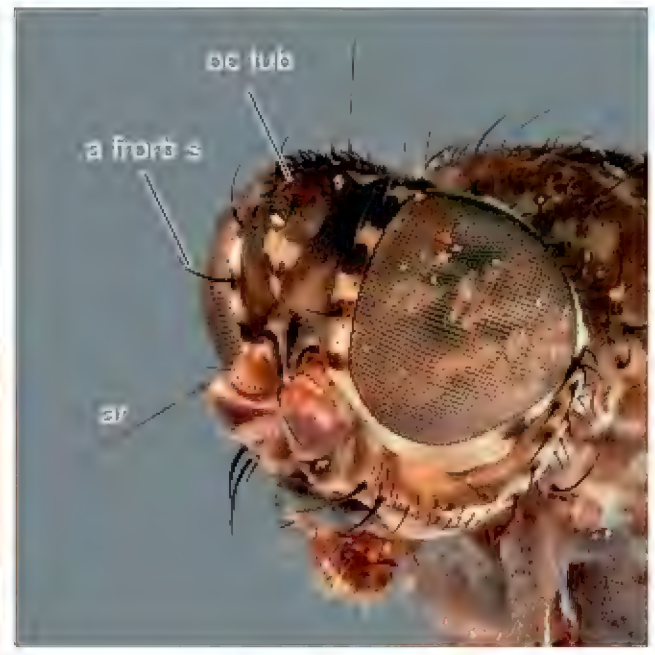
Economic significance

No species of economic significance are currently known.

Classification

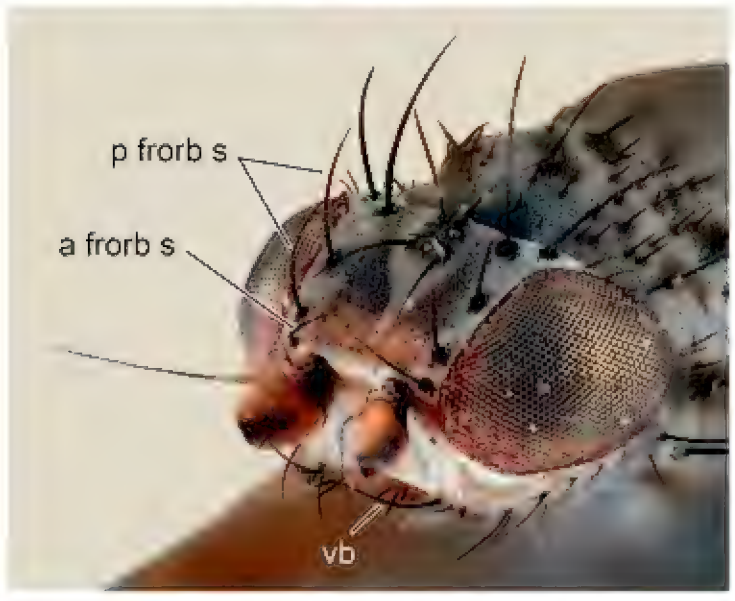
The traditional view (McAlpine 1989: 1455), suggests that Odiniidae form a monophyletic group with Agromyzidae and non-Afrotropical Fergusoninidae (suprafamily Agromyzoinea), within the superfamily Opomyzoidea. Using the perceived acalyptrate groundplan, McAlpine (1989: 1458) cited several synapomorphies, including the more dorsally located prothoracic spiracles of the larvae. There are two monophyletic lineages, the Agromyzidae + Fergusoninidae and the Odiniidae. Odiniids appear to be the more generalised representative of the Agromyzoinea, with larval mouthparts simpler, the prothoracic spiracles more dorsolaterally located and the larval habitats within galleries of wood-boring insects, rather than as primary tissue invaders of living plants. Odiniids were originally considered as a subfamily of Agromyzidae, until Hendel (1922–1923, 1928: 102), recognised them as a separate family. Hennig (1958) recognised odiniids and agromyzids as sister-taxa, but it was not until Spencer (1969) that specific character evidence

22 *Traginops* ♀



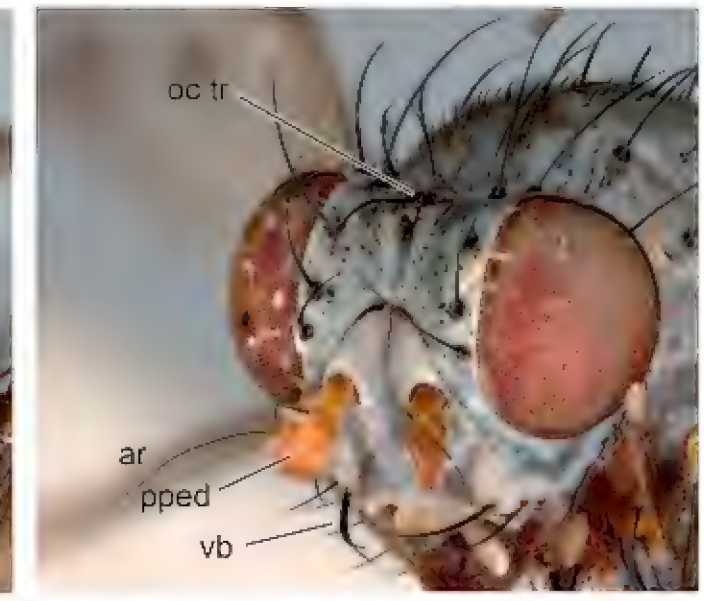
23 *Traginops* ♀

24 Undescribed genus A ♀



25 Undescribed genus A ♀

26 Undescribed genus B ♀



27 Undescribed genus B ♀

Figs 83.22–27. Heads of Odiniidae: (22) *Traginops* sp., frontal view ♀; (23) same, lateral oblique view; (24) Undescribed genus A, frontal view ♀; (25) same, lateral oblique view; (26) Undescribed genus B (*Odinia connecta* Cogan), frontal view ♀; (27) same, lateral oblique view. Figs 26, 27 (photographs © Trustees of the Natural History Museum, London).

Abbreviations: a frorb s – anterior fronto-orbital seta; ar – arista; lun – lunule; oc s – ocellar seta; oc tr – ocellar triangle; oc tub – ocellar tubercle; p frorb s – posterior fronto-orbital setae; pped – postpedicel; vb – vibrissa.

was applied to support this relationship, citing the strong phallapodeme, modified hypandrium, the form of the surstyli, the whole general terminalia arrangement and the presence of scutellar setulae in several odiniid genera and the more early-branching agromyzid genera, such as *Selachops* Wahlberg. Despite this, Griffiths (1972: 220) considered odiniids to belong in his Tephritoinea, entirely separated from its current placement. Although this traditional viewpoint is useful, more recent DNA studies (Wiegmann *et al*. 2011; Winkler *et al*. 2010), are not so clear-cut and determining the actual relationships of Odiniidae to other families requires further clarification.

The monophyly of Odiniidae is supported by the absence of an ejaculatory apodeme, the presence of several setae on the katepisternum and the presence of a preapical dorsal seta on one or more tibiae (McAlpine 1989: 1458). The family is divided into two subfamilies, Odiniinae and Traginopinae. For the Afrotropical odiniids, only *Afrodinia*, *Odinia* and Undescribed genus A represent the Odiniinae, while the remaining genera, *Coganodinia*, *Traginops* and Undescribed genera B and C, are in the Traginopinae. Several characters support this division, including the shape of the head, with the odiniines having a distinctly angulate frons to face, while the traginopines have the frons more or less sloping in line with the face; the position of the ocellar triangle, with the odiniines having the posterior ocelli in line with the inner vertical setae and the traginopines having the ocellar triangle more anteriorly placed.

Only a single fossil species, *Protodinia electrica* Hennig, 1965, has been described from Baltic amber. However more

28 Undescribed genus C ♂ | 29 Undescribed genus C ♂ | 30 *Afrodinia* ♂

31 *Traginops* sp. ♀ | 32 Undescribed genus B ♂ | 33 Undescribed genus C ♂

Figs 83.28–33. Heads of Odiniidae: (28) Undescribed genus C (*Paratraginops ruwenzoricus* Cogan), frontal view ♂; (29) same, lateral oblique view; (30) *Afrodinia* sp., lateral view ♂; (31) *Traginops* sp., lateral view ♀; (32) Undescribed genus B (*Odinia penrithorum* Cogan), lateral view ♂; (33) Undescribed genus C (*Paratraginops ruwenzoricus* Cogan), lateral view ♂. Figs 28, 29, 32, 33 (photographs © Trustees of the Natural History Museum, London).

Abbreviations: a frorb s – anterior fronto-orbital seta; ar – arista; fr – frons; gn – gena; gn s – genal seta; i vt s – inner vertical seta; lun – lunule; o vt s – outer vertical seta; oc tr – ocellar triangle; oc tub – ocellar tubercle; pprn – postpronotum; vb – vibrissa.

than 25 specimens of Dominican amber odiniids, mostly in the genus *Odinia*, are known to the writer. No Afrotropical fossil odiniid specimens are known.

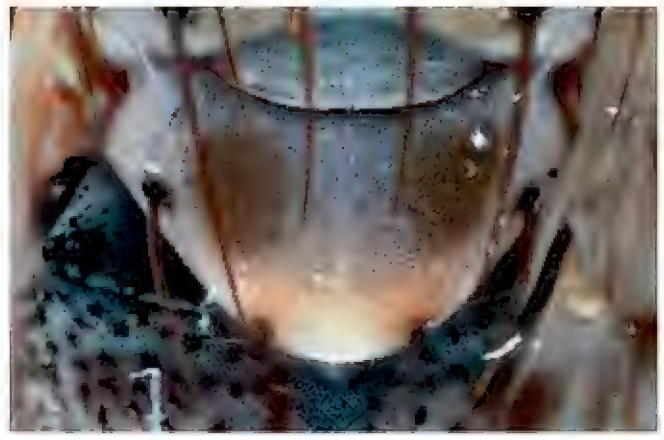
Identification

Only a few key resources are necessary for identifying the described species of Odiniidae, although many species remain undescribed. Hennig (1969) provided an identification key to the genera of the world, with descriptions or re-diagnoses of several genera and their species, but without identification keys to species. Cogan (1975) provided keys and descriptions for the known Afrotropical odiniid fauna. Sabrosky (1959) revised the genus *Odinia* for the New World, including descriptions of taxa and identification keys to species (although numerous species remain undescribed). For the Neotropical Region, Prado (1973) reassessed the described taxa, described several new taxa and provided identification keys to species and adequate drawings of diagnostic characteristics. McAlpine (1987: 866) and Papp (1998: 240) provided identification keys to the genera of the Nearctic and Palaearctic Regions, respectively. Gaimari (2007, 2010: 1052) provided an identification key to the currently described New World genera and Carvalho-Filho *et al*. (2009) concatenated several published keys to present a unified identification key to the described Neotropical species. Several new genera are currently recognised from various parts of the world that fall outside the below identification key, although the known Afrotropical genera are all included. Odiniidae are best micropinned in the field for later double-mounting (see Chapter 2).

34 *Afrodinia* ♂

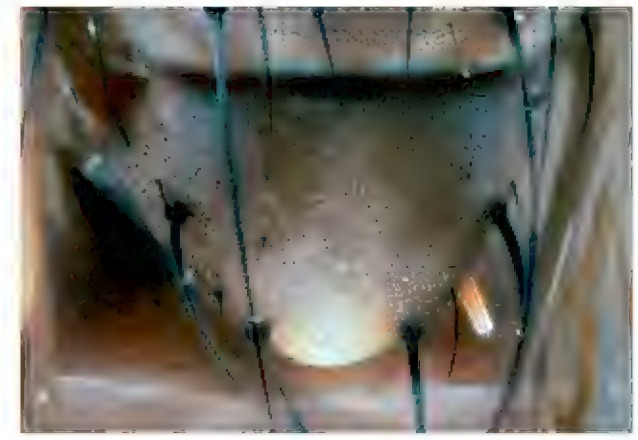
35 *Traginops* ♀

36 Undescribed genus B ♀



37 *Odinia* ♂

38 *Traginops* ♀



39 Undescribed genus C ♀

Figs 83.34–39. Thoracic pleura and scutella of Odiniidae: (34) thoracic pleura of *Afrodinia* sp., lateral view ♂; (35) same, *Traginops* sp. ♀; (36) same, Undescribed genus B (*Odinia connecta* Cogan) ♀; (37) scutellum of *Odinia* sp., dorsal view ♂; (38) same, *Traginops* sp. ♀; (39) same, Undescribed genus C ♀. Fig. 36 (photograph © Trustees of the Natural History Museum, London).

Abbreviations: anepst – anepisternum; kepst – katepisternum; pprn – postpronotum; prepst – proepisternum; prepst s – proepisternal seta.

Key to genera of Afrotropical Odiniidae

1. Head (viewed in profile), with frons flat to slightly concave, meeting lunule at distinct angle (*e.g.*, Figs 10, 30); ocellar triangle never on tubercle (*e.g.*, Fig. 20); scutellar disc never setulose (*e.g.*, Fig. 37) (ODINIINAE) 2

– Head (viewed in profile), with frons arched, sloping through lunule (*e.g.*, Figs 32, 33); ocellar triangle sometimes on weak (*e.g.*, Fig. 33) or strong tubercle (*e.g.*, Fig. 31); scutellar disc sometimes setulose (*e.g.*, Figs 38, 39) (TRAGINOPINAE) 4

2. Thorax with mesonotum with 5 dorsocentral setae (1 + 4) and 5 strong acrostichal setae (Fig. 7); wing (Fig. 42) with crossvein *dm–m*; vein R_{4+5} ending at or near wing tip . . . . . *Odinia* Robineau-Desvoidy

– Thorax with mesonotum with 4 dorsocentral setae (1 + 3), without acrostichal setae (*e.g.*, Fig. 3), except sometimes for prescutellar acrostichal seta (*e.g.*, Fig. 11); wing (*e.g.*, Figs 40, 44) without crossvein *dm–m*; vein R_{4+5} ending before wing tip, closer to tip of vein R_{2+3} 3

3. Head (Figs 16, 17), scutum and scutellum (Figs 3, 34) strikingly marked with velvety black and glossy black patches; thorax without prescutellar acrostichal seta (Fig. 3); katepisternum with 2 strong setae (Fig. 34) . . . . . *Afrodinia* Cogan

– Head, scutum, scutellum and body in general entirely pruinose, lacking glossy or velvety patches (Figs 10, 24, 25); thorax with prescutellar acrostichal seta (Fig. 11); katepisternum with 3 strong setae (as in Fig. 36) . . . . . Undescribed genus A

4. Head with ocellar triangle not on raised tubercle (*e.g.*, Figs 19, 27, 32); anterior fronto-orbital seta inserted below level of upper edge of lunule (*e.g.*, Figs 18, 26); thorax with postpronotum with 1 seta (Fig. 36); scutellum without setulae on disc (as in Fig. 37); costal wing vein (C) ending at vein R_{4+5} (*e.g.*, Figs 41, 45) 5

– Head with ocellar triangle set on tubercle (*e.g.*, Figs 22, 33); anterior fronto-orbital seta inserted at or above level of upper edge of lunule (*e.g.*, Figs 23, 28); thorax with postpronotum with 3 setae (*e.g.*, Fig. 35), although 2 may be small; scutellum with setulae on disc (*e.g.*, Figs 38, 39); costal wing vein (C) ending at vein M_1 (*e.g.*, Figs 43, 46) 6

5. Wing without crossvein *dm–m* (Fig. 41); thorax with mesonotum with 4 dorsocentral setae (1 + 3) (Fig. 5); without prescutellum . . . . . *Coganodinia* Gaimari & Mathis

– Wing with crossvein *dm–m* (Fig. 45); thorax with mesonotum with 5 dorsocentral setae (1 + 4) (Fig. 15); with prescutellum (Fig. 15) . . . . . Undescribed genus B

6. Head with large ocellar tubercle, conspicuously raised above upper eye margin (Fig. 31); antennal arista pubescent (Figs 23, 31); thorax with postpronotum with 3 strong setae (Fig. 35); scutellum with dense patch of setulae on disc (Fig. 38) . . . . . *Traginops* Coquillett

– Head with small ocellar tubercle, slightly higher than anterior ocellus (Fig. 33); antennal arista plumose (Figs 29, 33); thorax with postpronotum with 1 strong seta between 2 shorter, finer setae (Fig. 13); scutellum with sparse setulae on disc (Fig. 39) . . . . . Undescribed genus C

Synopsis of the fauna

Although a small family, with 74 species and subspecies in 16 extant genera, Odiniidae have only two widespread genera. Most are restricted in their distribution to only one or two faunal regions. Only *Odinia* is virtually cosmopolitan, being found on all continents, except Antarctica (noting that only undescribed species are known from the Afrotropics and Australasia). The genus *Traginops* is also widely distributed, but is notably absent from the Neotropical Region (noting that only undescribed species are known from Australasia). The remaining genera are regionally restricted, including five that are endemic to the Afrotropics. Despite this, the described Afrotropical fauna is remarkably small (only eight species in five genera), although there are new species recognised in some. Two additional genera are recorded here, despite their having no described species in the region. The rarity of encountering specimens of the family likely accounts for the apparent paucity of species. Cogan (1975) is the only work with identification keys to species for Afrotropical taxa and is useful, with the caveat that new species may not be able to be differentiated, so should be used with caution. All of the described species below are treated in that work. Note, in diagnosing the genera below, all the odiniine genera have the frons held at a distinct angle from the face in profile, while the traginopine genera have the frons arched and sloping through the face in profile.

***Afrodinia* Cogan** (Odiniinae)**.** An endemic genus of two described species, *A. deemingi* Cogan, 1975 and *A. medleri* Cogan, 1975, both described from Nigeria, the former from the north-central part and the latter from the south-western coastal area. Several undescribed species are known from Namibia and South Africa (including eastern South Africa near

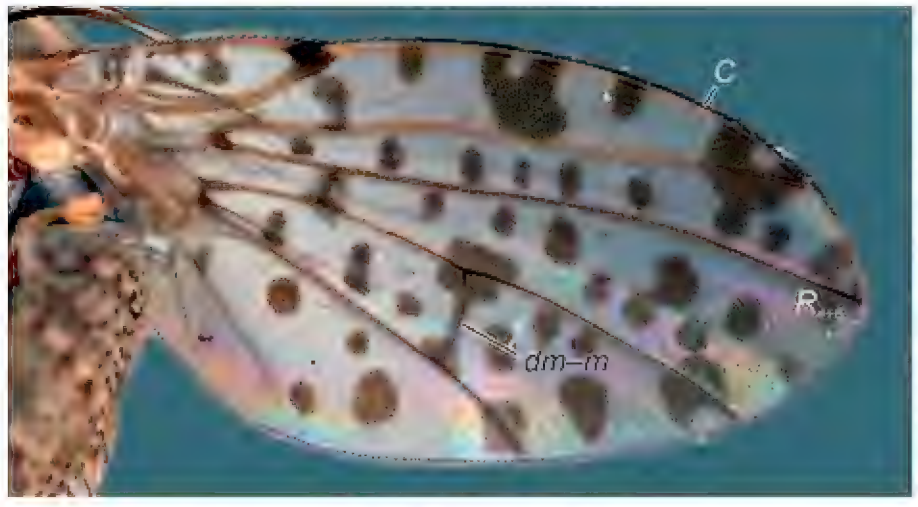
the Mozambique border). The habitat requirements of this genus appear broad, given their presence in wet lowland tropical forest and the drier mid-elevation parts of Nigeria and through the arid parts of south-western and Southern Africa. At least four new species are known and given the breadth of their habitats, more are to be expected. This genus is easily separated from other odiniine genera by the presence of velvety and glossy black patches on the head, scutum and scutellum, the lack of a prescutellar acrostichal seta and possession of only two strong katepisternal setae. Like Undescribed genus A, species of *Afrodinia* lack wing crossvein *dm–m* and vein R_{4+5} ends closer to the tip of vein R_{2+3} than to the wing tip. The puparium of an *Afrodinia* species was described by Kirk-Spriggs & Barraclough (2009), the larvae feed upon *Vachellia karroo* gum in the tunnels of wood-boring beetles. The two described species can be identified using the identification key provided by Cogan (1975), but this should be used with caution, as there are several undescribed species.

***Coganodinia* Gaimari & Mathis** (Traginopinae)**.** An endemic monotypic genus, with the single described species, *C. cornesi* (Cogan, 1975), recorded from southern Nigeria and into Cameroon. No undescribed species are currently recognised, but are possible. Given its distribution, this genus appears to prefer lowland tropical forest habitats. This is the only Afrotropical traginopine genus that lacks wing crossvein *dm–m*. Along with Undescribed genus B, this genus lacks an ocellar tubercle and has the costal wing vein (C) ending at vein R_{4+5}. The biology and immature stages remain unknown.

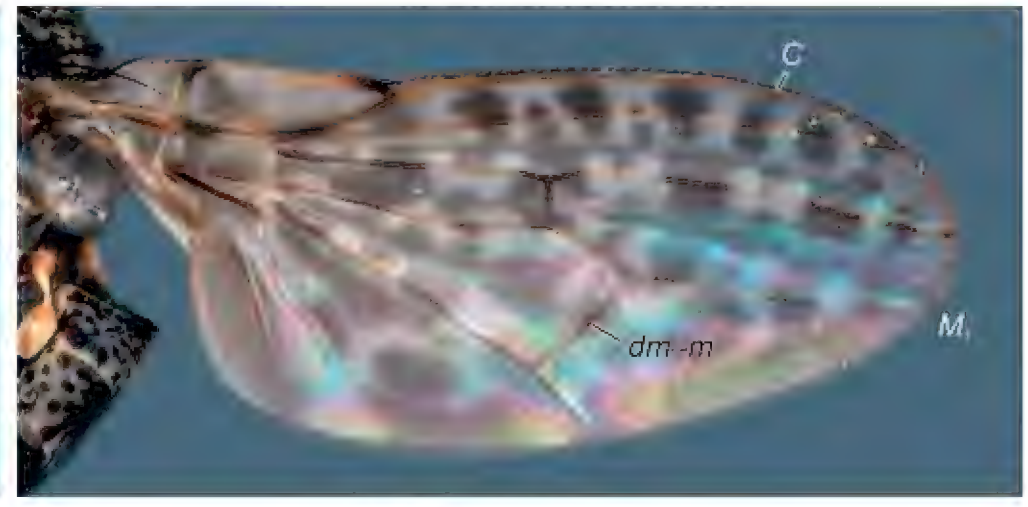
***Odinia* Robineau-Desvoidy** (Odiniinae)**.** A virtually cosmopolitan genus of 26 described species, recorded from all zoogeographical regions, except Antarctica. The genus makes up about one-third of the described species in the family. Despite this, no described species of *Odinia* are currently known from the Afrotropical Region (although a few species in other genera had been originally described as *Odinia*). The entire Afrotropical fauna of this genus is, therefore, made up of undescribed species, including those known from Cameroon, Kenya, Malawi, Namibia, Nigeria, Tanzania and United Arab Emirates (Gaimari 2011: 780). As an indication of the rarity of this genus (and family) in the Afrotropics, each of these localities is known from a single specimen, with the exception of two from Kenya. The genus appears rather widespread and is known from a variety of habitats in the Afrotropics, so the number of new species is probably quite high, but knowledge of these is limited, due to their rarity in collections. The genus is easily recognised by the presence of five dorsocentral and five acrostichal setae. It is the only Afrotropical odiniine genus with crossvein *dm–m* present and the tip of R_{4+5} being near the wing tip. Immature stages are partially known (Kato 1952; Krivosheina 1981: 152; Lewis 1979; Yang 1984; Zubkov & Kovalev 1975).

40 *Afrodinia* ♂

41 *Coganodinia* ♀



42 *Odinia* ♀



43 *Traginops* ♀

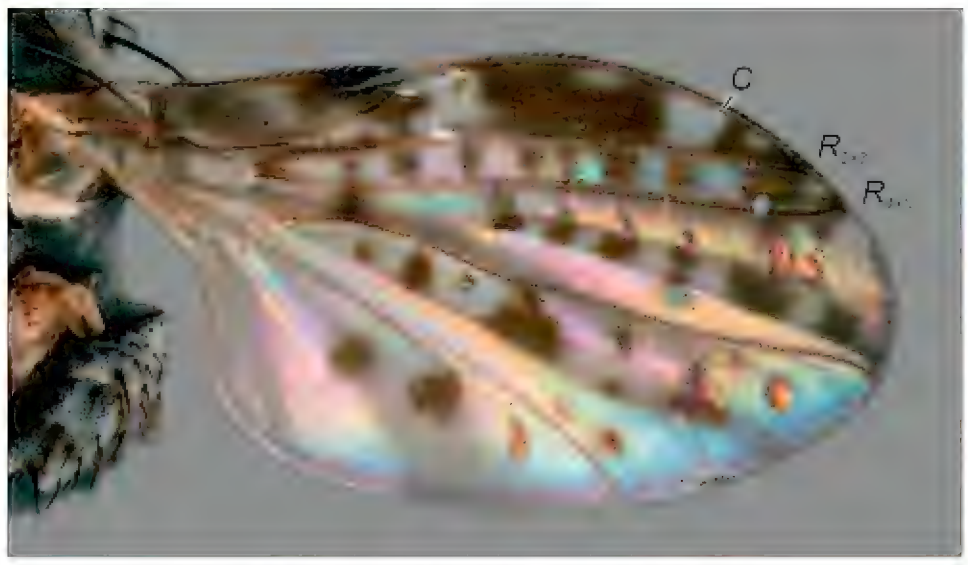
Figs 83.40–43. Wings of Odiniidae (dorsal views): (40) *Afrodinia* sp. ♂; (41) *Coganodinia cornesi* (Cogan) ♀; (42) *Odinia* sp. ♀; (43) *Traginops* sp. ♀. Fig. 41 (photograph © Trustees of the Natural History Museum, London).

Abbreviations: *C* – costal vein; *dm–m* – discal medial crossvein; M_1 – first branch of media; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius.

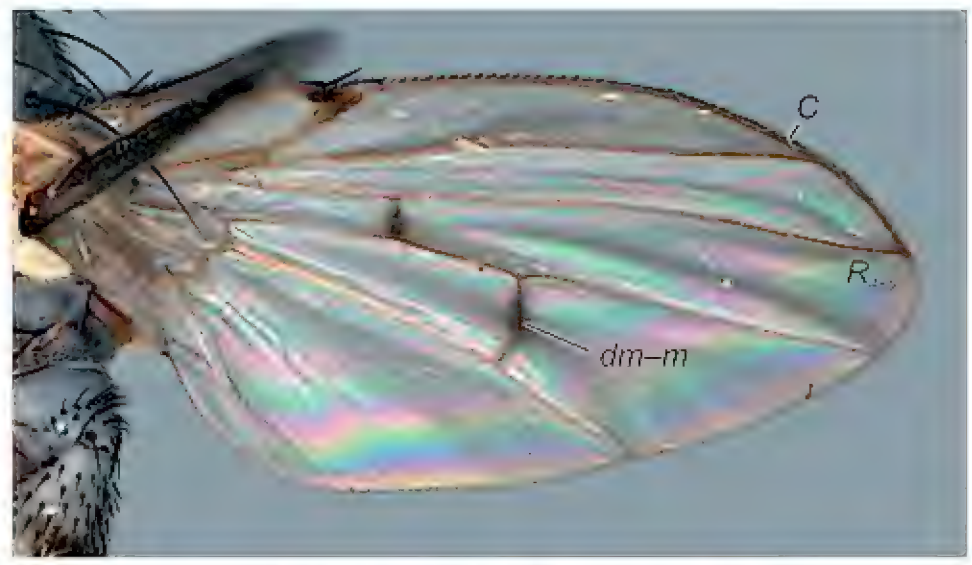
***Traginops* Coquillett** (Traginopinae)**.** A very widespread genus of eight described species, occurring in the Afrotropical, Holarctic and Oriental Regions. Two species occur in the Afrotropics, *T. moremii* Cogan, 1975, known only from the Okavango Delta area of Botswana and *T. shewelli* Cogan, 1975, from farther north in the coastal area of Lake Victoria in Uganda. At least one undescribed species is known from Ethiopia and more undescribed species are to be expected. The genus is easily separated from other Afrotropical genera by the large, conspicuous ocellar tubercle, the presence of a patch of setulae on the dorsal part of the scutellum and the wing with costal vein (C) ending at vein M_1. Although both Undescribed genus C and *Traginops* have three postpronotal setae, only in *Traginops* are they all equally strong. Immature stages are partially known (Shewell 1960). The two described species can be identified by reference to the identification key in Cogan (1975), bearing in mind at least one undescribed species is known from the region.

Undescribed genus A (Odiniinae)**.** An endemic genus known only from undescribed species. Two species are known from Kenya, one from the southern coastal area near the Tanzania border and one from the west-central part of the country, near the border with Uganda, and several more from Madagascar. The species from Madagascar appear readily collected in moderate numbers by Malaise trapping. More undescribed species are expected. This genus is easily separated from other Afrotropical odiniines, by the combination of absence of any velvety markings, having four dorsocentral setae, absence of wing crossvein *dm–m* and having vein R_{4+5} ending closer to R_{2+3} than to the wing tip. As with *Odinia*, the genus has a strong prescutellar acrostichal seta, but unlike *Odinia*, there are no additional strong acrostichal setae. The biology and immature stages remain unknown.

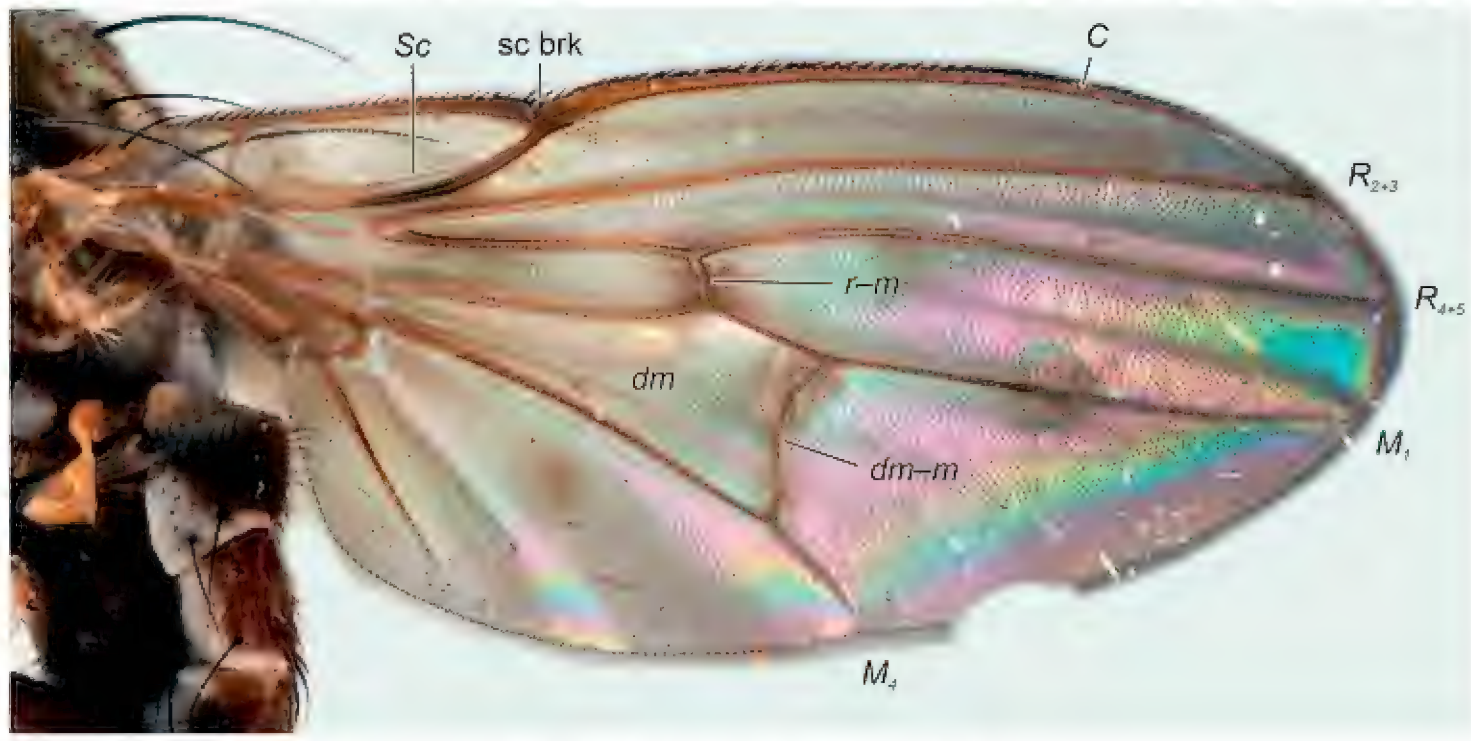
Undescribed genus B (*Odinia sensu* Cogan) (Traginopinae)**.** An endemic genus with two described species, both



44 Undescribed genus A ♀



45 Undescribed genus B ♀



46 Undescribed genus C ♀

Figs 83.44–46. Wings of Odiniidae (dorsal views): (44) Undescribed genus A ♀; (45) Undescribed genus B (*Odinia connecta* Cogan) ♀; (46) Undescribed genus C ♀. Fig. 45 (photograph © Trustees of the Natural History Museum, London).

Abbreviations: *C* – costal vein; *dm* – discal medial cell; *dm–m* – discal medial crossvein; M_1 – first branch of media; M_4 – fourth branch of media; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Sc* – subcostal vein; sc brk – subcostal break.

of which were originally described in the genus *Odinia*. *Odinia connecta* Cogan, 1975, is known from Kaduna State in the north-central part of Nigeria, which has a seasonally wet climate. The species was subsequently recorded from Gambia (Schacht 2000), but the record may represent an undescribed species. The other species, *O. penrithorum* Cogan, 1975, is known only from Namibia, in the north-western part at the southern border of Kaokoveld, a considerably more arid habitat than that of *O. connecta*. This is the only Afrotropical traginopine genus that has five dorsocentral setae and a prescutellum. Along with *Coganodinia*, this genus lacks an ocellar tubercle and has costal wing vein (C) ending at vein R_{4+5}. The biology and immature stages remain unknown.

47 *Odinia* ♀

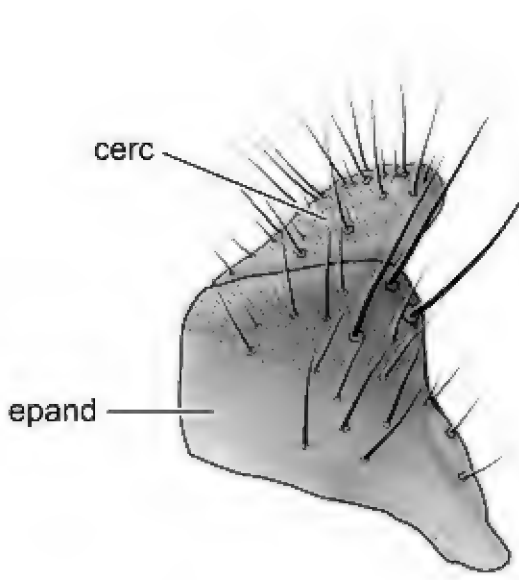
48 *Traginops* ♀

49 Undescribed genus B ♀

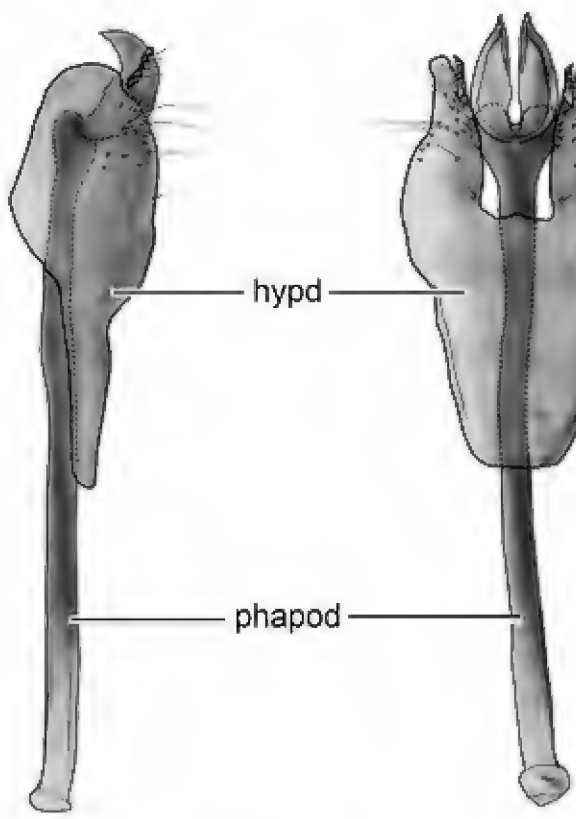
50 Undescribed genus C ♀

Figs 83.47–50. Abdomens of Odiniidae (dorsal views): (47) *Odinia* sp. ♀; (48) *Traginops* sp. ♀; (49) Undescribed genus B (*Odinia connecta* Cogan) ♀; (50) Undescribed genus C (*Paratraginops ruwenzoricus* Cogan) ♂. Figs 49, 50 (photographs © Trustees of the Natural History Museum, London).

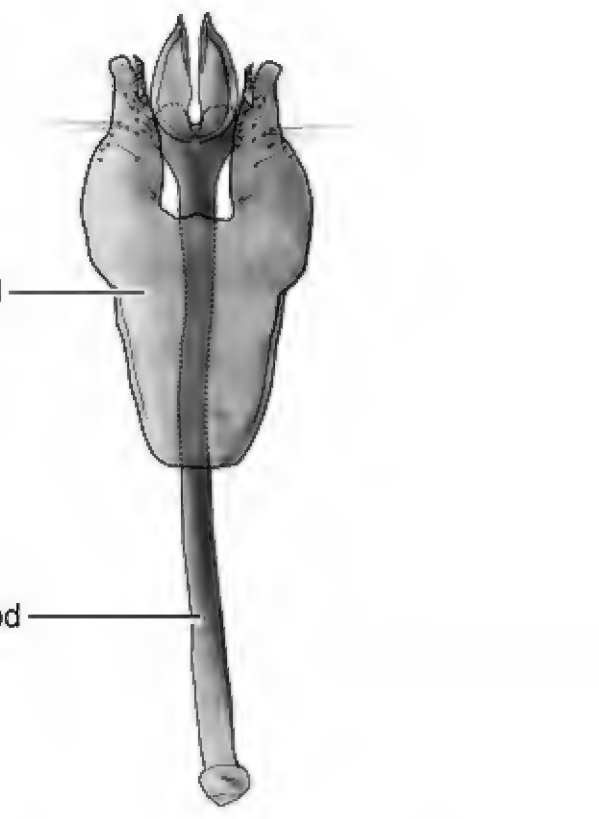
Undescribed genus C (*Paratraginops sensu* Cogan) (Traginopinae)**.** An endemic, currently monotypic genus, with the single species, *Paratraginops ruwenzoricus* Cogan, 1975, known only from Uganda, in the foothills of the Ruwenzori Mountains. At least one undescribed species is known from Malawi. This genus is easily separated from other Afrotropical traginopines by the combination of having a small protuberant ocellar triangle (although much smaller than in *Traginops*) and a plumose arista. Although both Undescribed genus C and *Traginops* have three postpronotal setae and setulae on the scutellum, in this genus the upper and lower postpronotal setae are much weaker than the central seta and the scutellar setulae are sparse and inconspicuous. This genus also shares the costal wing vein (*C*) ending at vein M_1 with *Traginops*. The biology and immature stages remain unknown.



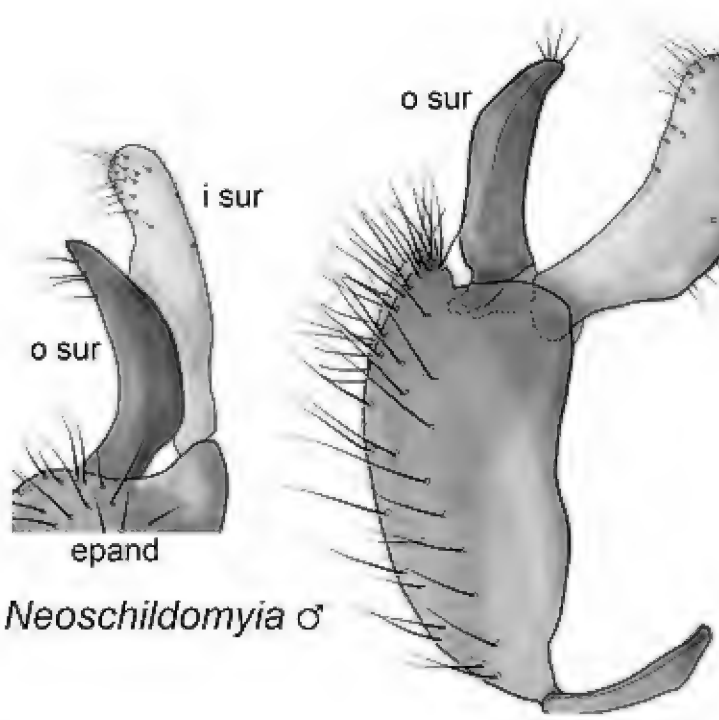
51 *Helgreelia* ♂



52 *Helgreelia* ♂

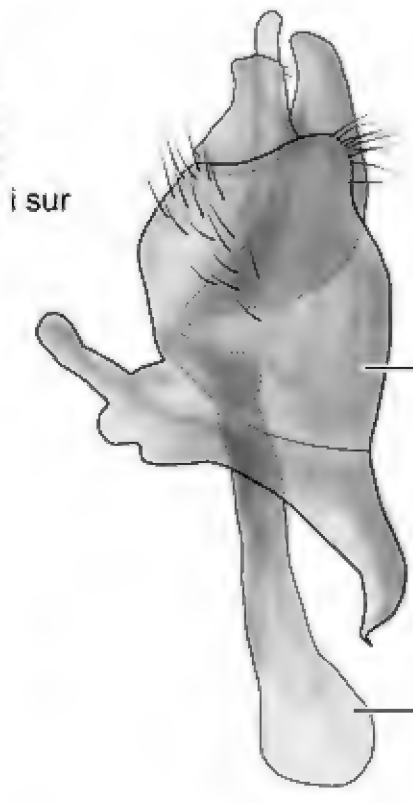


53 *Helgreelia* ♂

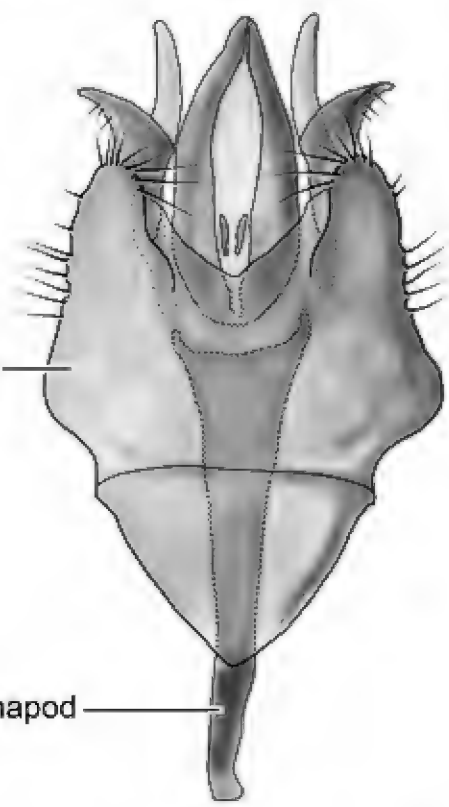


54 *Neoschildomyia* ♂

55 *Neoschildomyia* ♂



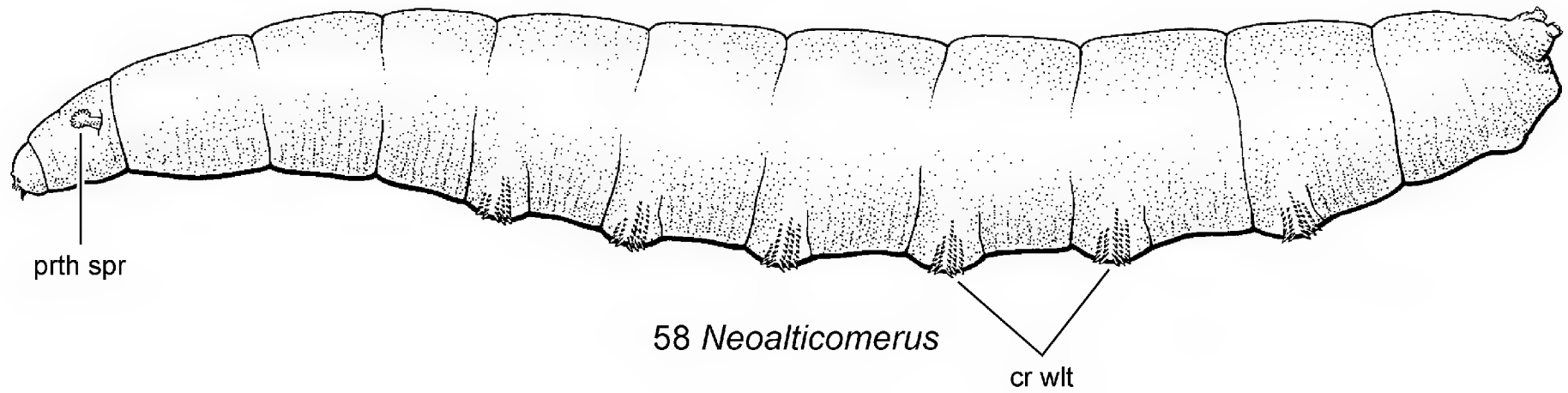
56 *Neoschildomyia* ♂



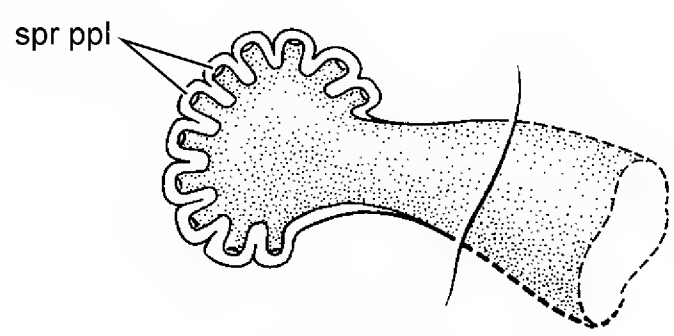
57 *Neoschildomyia* ♂

Figs 83.51–57. Male terminalia of Odiniidae: (51) epandrial complex of *Helgreelia parkeri* Gaimari, lateral view (non-Afrotropical); (52) same, hypandrium and phallic complex, lateral view; (53) same, ventral view; (54) epandrium and inner and outer surstyli of *Neoschildomyia fusca* Gaimari, lateral view (non-Afrotropical); (55) same, dorsal view; (56) same, hypandrium and phallic complex, lateral view; (57) same, ventral view. Figs 51–57 (Gaimari 2007, figs 4A–C, 5A–D).

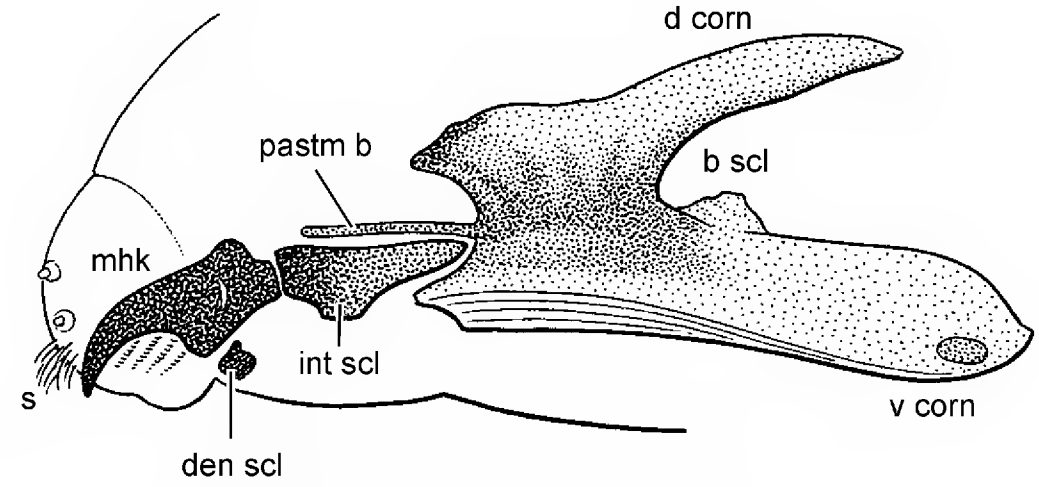
Abbreviations: cerc – cercus; epand – epandrium; hypd – hypandrium; i sur – inner surstylus; o sur – outer surstylus; phapod – phallapodeme.



58 *Neoalticomerus*



59 *Neoalticomerus*



60 *Neoalticomerus*

Figs 83.58–60. Immature stages of Odiniidae: (58) larva habitus of *Neoalticomerus seamansi* Shewell, lateral view (non-Afrotropical); (59) prothoracic spiracle, lateral view; (60) head segment and cephaloskeleton, lateral view. Figs 58–60 (McAlpine 1987, figs 7–9).

Abbreviations: b scl – basal sclerite; cr wlt – creeping welts; d corn – dorsal cornu; den scl – dental sclerite; int scl – intermediate sclerite; mhk – mouthhook; pastm b – parastomal bar; prth spr – prothoracic spiracle; s – setulae; spr ppl – spiracular papillae; v corn – ventral cornu.

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OPOMYZIDAE 84

(Opomyzid Flies)

Jan Willem A. van Zuijlen

Fig. 84.1. Female of *Opomyza petrei* Mesnil (non-Afrotropical) (photograph © S.A. Marshall).

Diagnosis

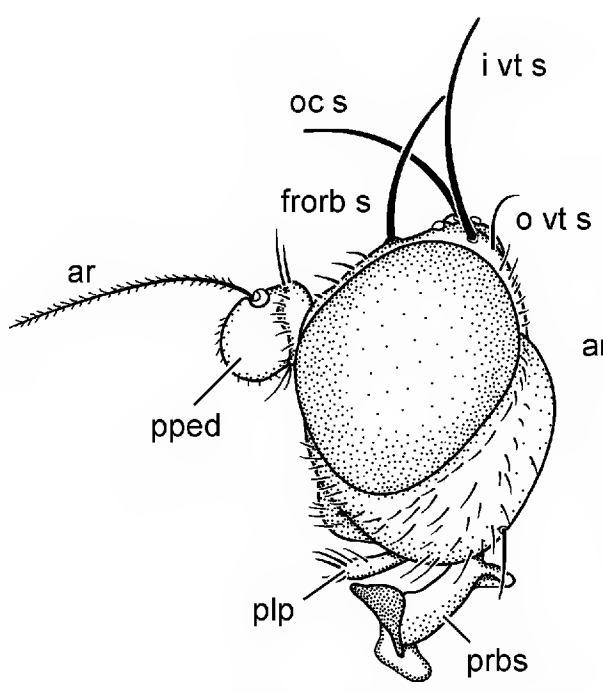
Small-sized (body length: 2–5 mm), slender, yellow, brown or blackish acalyptrate flies, with rather long and slender, more or less distinctly marked wings (Fig. 1).

Head (Figs 2, 3) about as broad as thorax, dorsally slightly angular in profile; compound eye large, almost round to ovoid, bare; frons broad, narrowing anteriorly, with more or less distinct ocellar triangle and frontal vitta; occiput slightly concave; face narrowing towards antennae, relatively flat to medially depressed; parafacial and gena narrow; clypeus small; antenna short; postpedicel with rounded apex, with short to long pubescence (Figs 2, 3); arista pubescent or dorsally plumose; cephalic chaetotaxy without postocellar setae, or if present (*Anomalochaeta* Frey), then divergent; strong inner and outer vertical setae; 1 strong reclinate fronto-orbital seta; ocellar setae strong; interfrontal setulae scattered; vibrissa absent, but one or more subvibrissae may be relatively strong; proboscis and palpus slender, the latter with some setae.

Thorax (Figs 4, 5) longer than wide; postpronotum well-defined; transverse suture laterally distinct; thoracic chaetotaxy (Figs 4, 5) with 1 postpronotal seta; 2 notopleural setae; 1 presutural seta; 1 supra-alar seta; 1 postalar seta; 0–1 intrapostalar seta; 1 presutural dorsocentral seta and 2–3 postsutural

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2021. Manual of Afrotropical Diptera. Volume 3. Brachycera—Cyclorrhapha, excluding Calyptratae. *Suricata* 8. South African National Biodiversity Institute, Pretoria; pp. 1903–1908.

dorsocentral setae; acrostichal setulae in 4–10 rows (Fig. 5); 1 anepisternal seta, anepisternum setulose; 1 basal and 1 apical scutellar marginal seta (Figs 4, 5); katepisternum with 1 seta and 1 or more stronger setulae in upper part (Fig. 4); prosternum setulose. Scutellum rounded, subtriangular (Figs 5, 6). Wing moderately broad (Fig. 7) to very narrow in stenopterous species (Fig. 8); alula and anal lobe reduced, but distinct if wing fully developed, absent if wing reduced; costal vein (*C*) with subcostal break; subcostal vein (*Sc*) reduced, fused with vein R_1, weakly developed in apical ½; crossvein *bm–m* present, but incomplete, leaving cells *bm* and *dm* entirely separated; cell *cua* present, but narrow; *CuA+CuP* short or absent; calypters reduced; halter normal or virtually without stem (in *Geomyza alluaudi* (Hendel, 1917)). Legs slender and setulose; tibiae without dorsal preapical setae; mid tibia with strong ventroapical seta.



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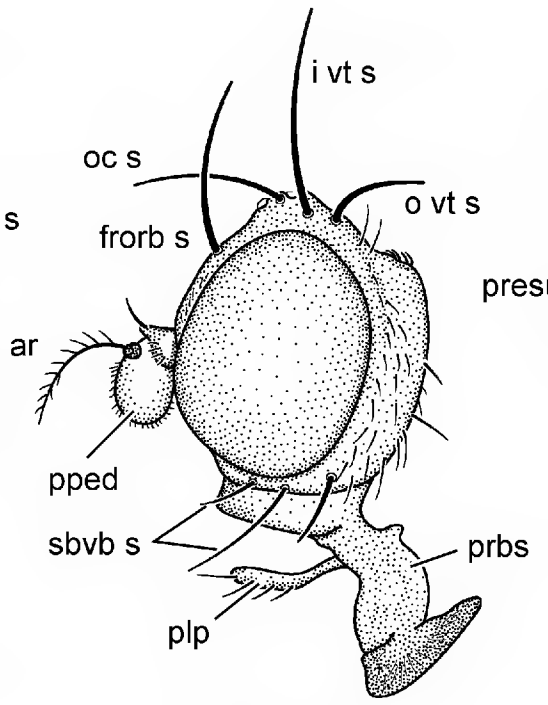

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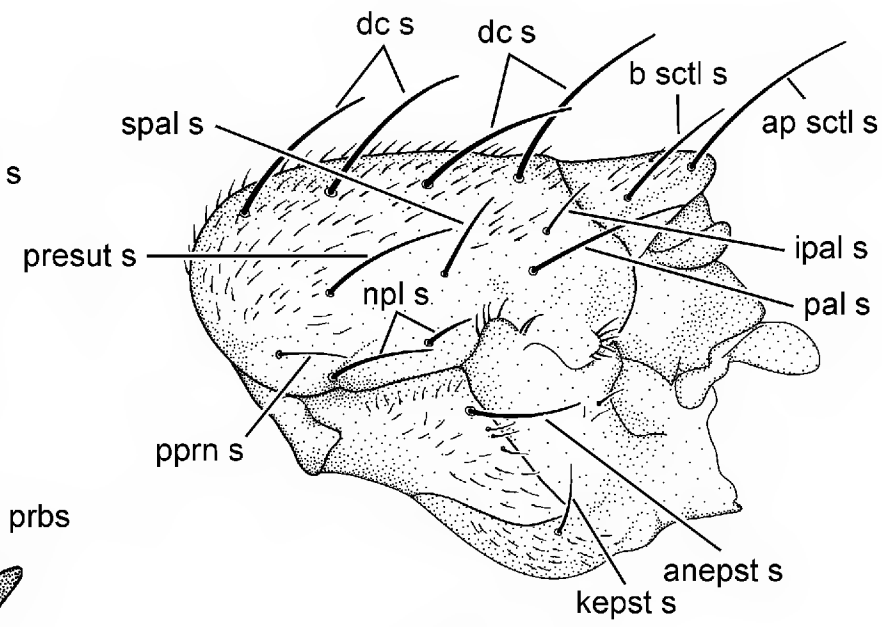

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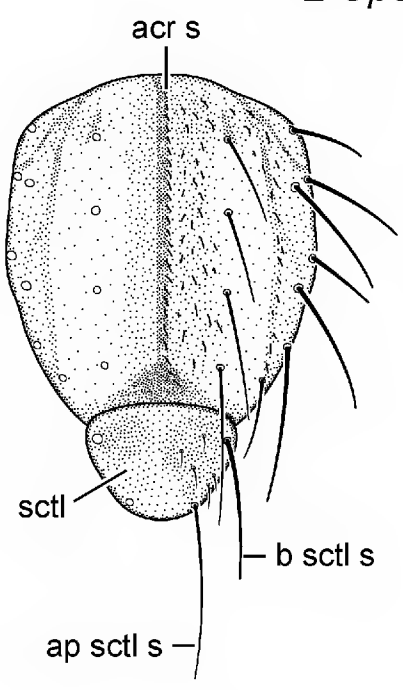
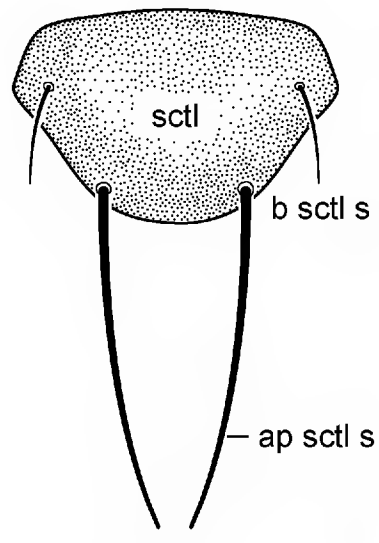
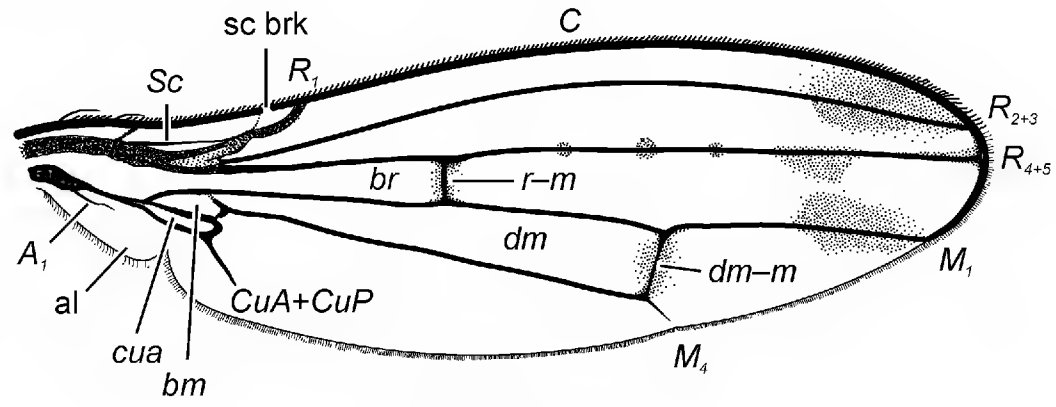


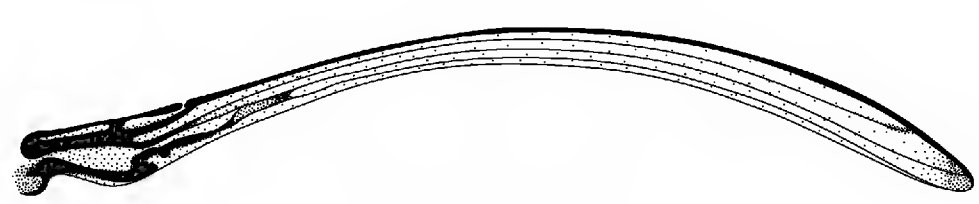
5 *Opomyza*



6 *Geomyza*



7 *Opomyza*



8 *Geomyza*

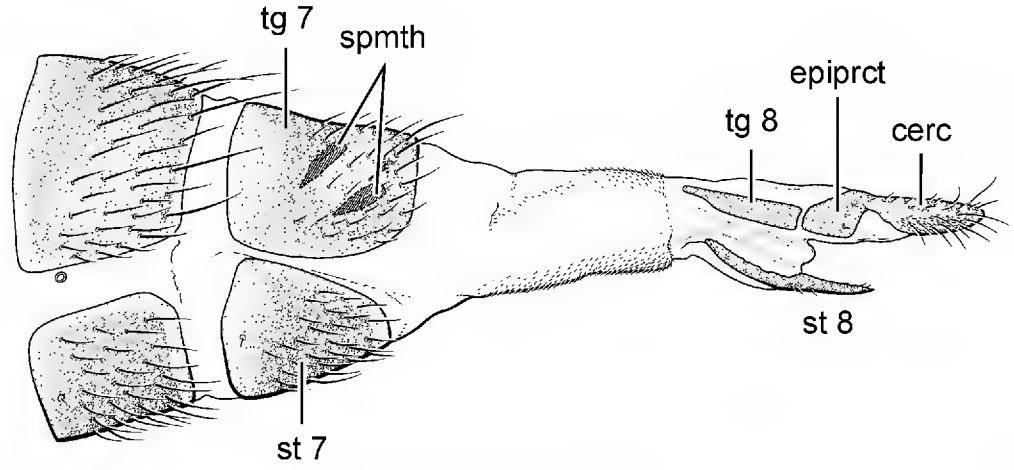
Figs 84.2–8. Heads, thoraces, scutellum and wings of Opomyzidae: (2) head of *Opomyza milleri* Barraclough, lateral view; (3) same, *Geomyza balachowskyi* Mesnil (non-Afrotropical); (4) thorax of *O. milleri*, lateral view; (5) same, *O. capensis* Stuckenberg, dorsal view (setation omitted on left side); (6) scutellum of *G. balachowskyi*, dorsal view; (7) wing of *O. milleri*, dorsal view; (8) same, *G. alluaudi* (Hendel).

Abbreviations: A_1 – first branch of anal vein; acr s – acrostichal setae; al – alula; anepst s – anepisternal seta; ap sctl s – apical scutellar seta; ar – arista; b sctl s – basal scutellar seta; *bm* – basal medial cell; *br* – basal radial cell; *C* – costal vein; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; dc s – dorsocentral setae; *dm* – discal medial cell; *dm–m* – discal medial crossvein; frorb s – fronto-orbital seta; ipal s – intrapostalar seta; i vt s – inner vertical seta; kepst s – katepisternal seta; M_1 – first branch of media; M_4 – fourth branch of media; npl s – notopleural seta; o vt s – outer vertical seta; oc s – ocellar seta; pal s - postalar seta; plp – palpus; pped – postpedicel; pprn s – postpronotal seta; prbs – proboscis; presut s – presutural seta; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; sbvb s – subvibrissal setae; *Sc* – subcostal vein; sc brk – subcostal break; sctl – scutellum; spal s – supra-alar seta.

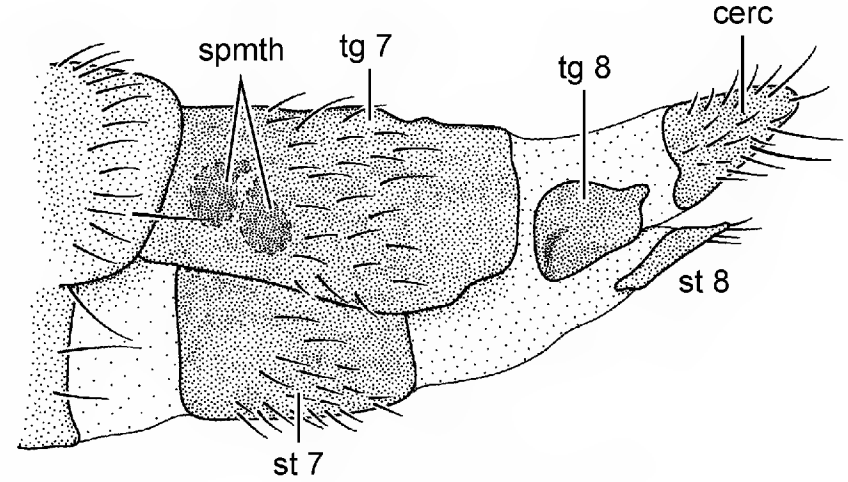
Abdomen with tergites and sternites unmodified, corresponding 6 pairs of spiracles (both sexes) inserted in membrane below tergites (Fig. 9); male preabdomen (Fig. 9) with 5 segments; tergite 6 absent (present and lying behind tergite 5 in *Anomalochaeta*); remnants of segments 6–8 forming segmental complex, consisting of short bare sternite 6 displaced to left, small to large bare sternite 7 displaced to left and large setulose dorsal, virtually symmetrical remnant of sternite 8; male terminalia (Fig. 9) largely symmetrical; epandrium ventrally produced on each side into short to moderately long surstylus, fused to epandrium; sclerotised part of inner surface of surstylus with apex produced into short spur or bearing short stout spines; cercus slender, joined by membrane in basal ½, with apical ½ sub-cylindrical to slightly flattened, projecting ventrally, sometimes as far as apex of surstylus; hypandrium deep, two halves posterodorsally and anteroventrally joined by narrow bridge; postgonite lying between base of phallus and inner posterior margin of hypandrium, slender, weakly sclerotised; phallic complex strongly sclerotised; phallapodeme long and slender; female abdomen (Figs 10, 11) with 7 well-developed segments; segment 8 separated from segment 7 by membrane; tergite 8 dorsomedially divided; sternite 8 undivided, very weakly sclerotised medially, or divided; epiproct fused to cercus (Fig. 10) or absent (Fig. 11); hypoproct absent; cercus flattened, 2–5 × as long as wide, setulose; 2 sclerotised, subspherical or elongate spermathecae present.

Opomyzidae are superficially similar to Clusiidae (see Chapter 81), but can be separated as follows: in Clusiidae the outer side of the pedicel has a triangular projection, but is straight in Opomyzidae and the subcostal wing vein in Clusiidae is complete, whereas it is incomplete in Opomyzidae. Opomyzidae also resemble Anthomyzidae (see Chapter 87), especially taxa with reduced cephalic chaetotaxy, *e.g.*, *Scelomyza* Séguy. They differ from species of the latter family in having the postocellar setae absent or divergent and the anepimeron setose (apart from substantial dissimilarities in the male and female terminalia).

9 *Geomyza* ♂



10 *Geomyza* ♀



11 *Opomyza* ♀

Figs 84.9–11. Male terminalia and female postabdomens of Opomyzidae: (9) male terminalia of *Geomyza lurida* (Loew), lateral view (non-Afrotropical); (10) same, female postabdomen; (11) same, *Opomyza capensis* Stuckenberg. Figs 9, 10 (Vockeroth 1987, figs 10, 11).

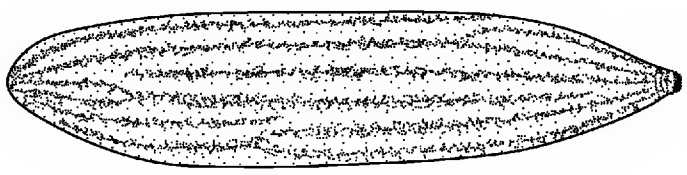
Abbreviations: basph – basiphallus; cerc – cercus; distph – distiphallus; epand – epandrium; epiprct – epiproct; gon – gonopod; hypd – hypandrium; pgt – postgonite; ph gd – phallic guide; phapod – phallapodeme; spmth – spermathecae; st – sternite; sur – surstylus; syntgst – syntergosternite; tg – tergite.

Biology and immature stages

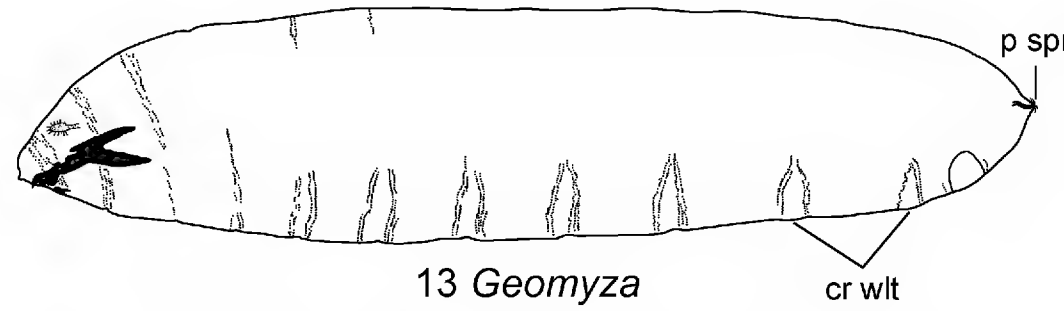
Adult Opomyzidae occur in cereal fields, meadows, pastures and hedges (Brunel 1998), but also in the grassy undergrowth of forests, both in dry and humid to wet habitats. Adults may live as long as three to six months and are uni- or bivoltine, overwintering in the larval or egg stage. The adults of some species have also been observed during the winter months.

Opomyzidae are phytophagous, larvae developing in grasses and cereals (Poaceae) and *Carex* and *Scirpus* (Cyperaceae). Eggs are deposited at the base of the stems of the host-plant and developing larvae penetrate the leaves and move to the heart of the plant. The external leaves of the host-plant remain green, but the central leaves turn yellow and die, causing damage referred to as "dead heart". The larvae pupariate outside the host-plant on the surface of the soil.

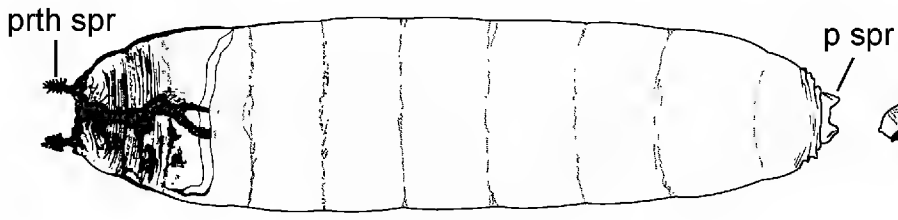
The egg of the Holarctic species *Geomyza tripunctata* Fallén, 1823 (Fig. 12) was described by Thomas (1938) and more recently by Ferrar (1987: 264). It is fusiform in shape and more broadly rounded at the posterior than at the anterior end, the anterior end being considerably thickened and drawn-out in the form of a plug. The chorion is white and glistening, slightly flattened on its ventral surface and the surface is marked by a series of longitudinal ridges and grooves. The entire surface is



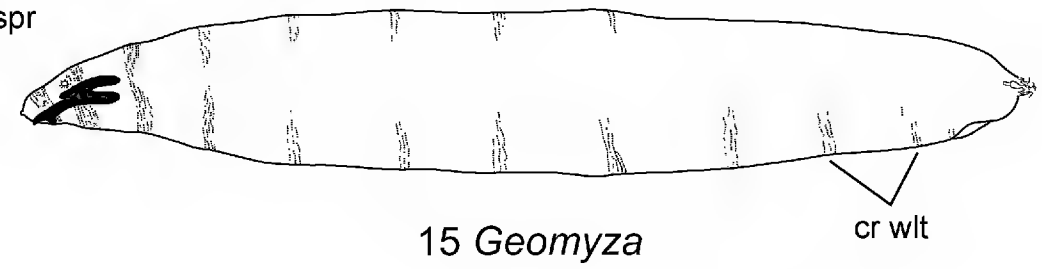
12 *Geomyza*



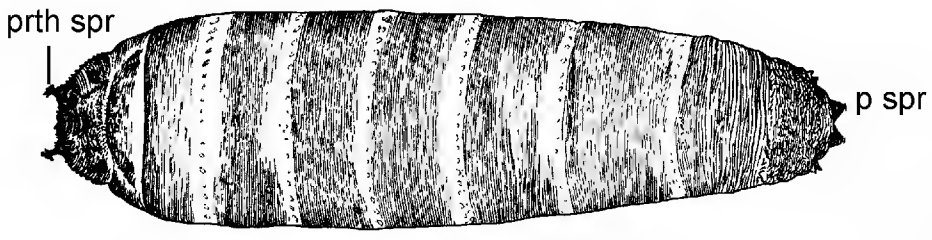
13 *Geomyza*



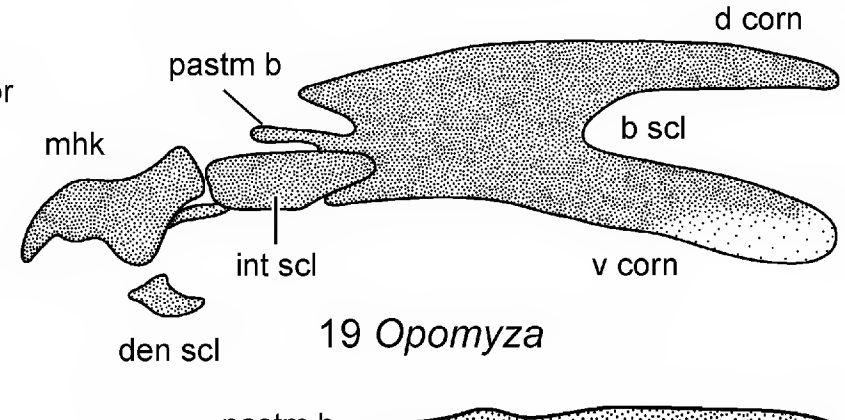
14 *Geomyza*



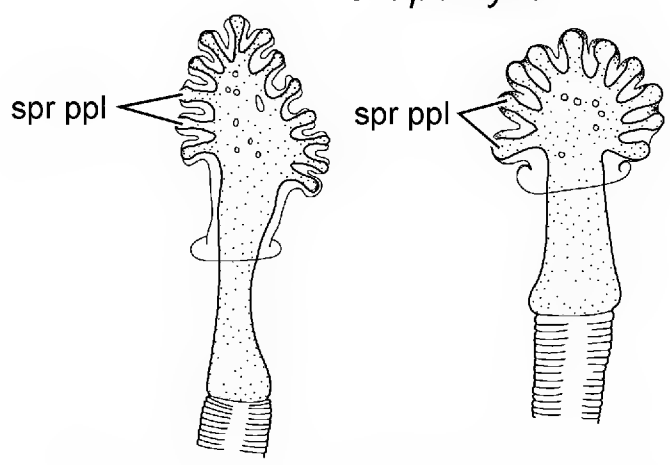
15 *Geomyza*



16 *Opomyza*

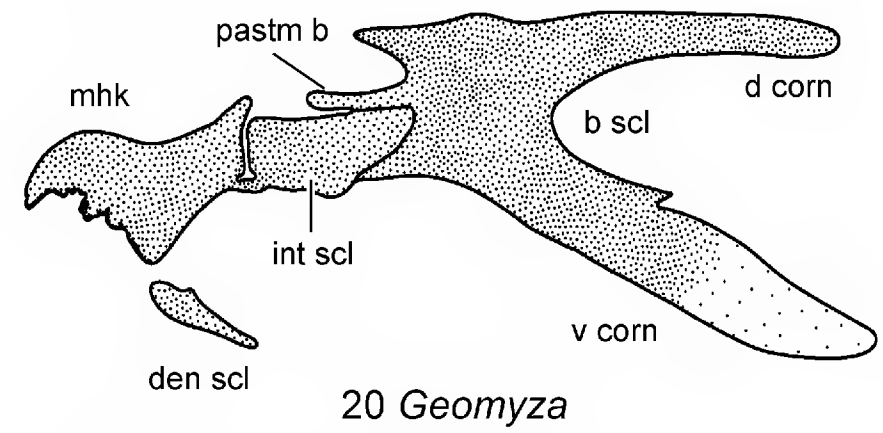


19 *Opomyza*



17 *Geomyza*

18 *Opomyza*



20 *Geomyza*

Figs 84.12–20. Immature stages of Opomyzidae (all non-Afrotropical): (12) egg of *Geomyza tripunctata* Fallén, lateral view; (13) same, larval habitus, lateral view; (14) puparium of *G. martineki* Drake, ventral view; (15) larval habitus of *Opomyza petrei* Mesnil, lateral view; (16) puparium of *O. florum* (F.), ventral view; (17) larval prothoracic spiracle of *G. tripunctata*, lateral view; (18) same, *O. petrei*; (19) same, cephaloskeleton, lateral view; (20) same, *G. tripunctata*. Fig. 12 (after Thomas 1934, fig. 9), Figs 13, 15, 17, 18–20 (after Nye 1958, figs 40, 24, 39, 23, 21, 37, respectively), Figs 14, 16 (after Balachowsky & Mesnil 1935, figs 875, 843, respectively).

Abbreviations: b scl – basal sclerite; cr wlts – creeping welts; d corn – dorsal cornu; den scl – dental sclerite; int scl – intermediate sclerite; mhk – mouthhook; p spr – posterior spiracle; pastm b – parastomal bar; prth spr – prothoracic spiracle; spr ppl – spiracular papillae; v corn – ventral cornu.

covered in a series of minute papillae, which are more numerous on the ridges than in the grooves.

Larvae of Palaearctic species (Figs 13, 15) were described by Nye (1958) and more extensively by Ferrar (1987: 264–265). The larva is creamy white to creamy yellow in colour, reaching a length of up to 8 mm and a diameter of 1 mm. The ventral creeping welts are formed of irregular broken rows of linearly grouped spicules and the posterior spiracular prominences are distinctly separated. The prothoracic spiracles are formed of small spiracular papillae, of an elongate rosette type in *Geomyza* Fallén (Fig. 17) and a rounder rosette type in *Opomyza* Fallén (Fig. 18). The cephaloskeleton (Figs 19, 20) is strongly sclerotised, with robust dentate mouthhooks, a distinct dental sclerite, a robust intermediate sclerite and a basal sclerite divided into a dorsal and ventral cornu.

The puparium (Figs 14, 16) was described for Palaearctic species by Balachowky & Mesnil (1935), Ferrar (1987: 265) and Thomas (1934). The puparium is dark brown, approximately cylindrical in shape and varies in length from 3.6–5.0 mm. The larval prothoracic spiracles remain protruding from the anterior end of the puparium and the cuticle of the posterior end is deeply wrinkled.

Economic significance

Although a number of opomyzid species have been reported to cause losses in cereals and grasslands in the Palaearctic Region (Balachowsky & Mesnil 1935; Krusteva *et al*. 2012; Mesnil 1931; Nye 1958; Thomas 1934), no economically relevant damage by Opomyzidae has been reported in the Afrotropical Region.

Classification

The Opomyzidae, belonging to the superfamily Opomyzoidea (see McAlpine 1989: 1454), are well-characterised as a monophyletic group (Griffiths 1972: 205). Following a thorough morphological cladistic analysis of fossil and recent genera, Roháček (1998) confirmed a sister-group relationship between the families Opomyzidae and Anthomyzidae. Roháček (1998) presumed the sister-pair Opomyzidae + Anthomyzidae most probably is derived from a clusiid-like ancestor. Because of their phytophagy, the Opomyzidae are considered to be the more specialised group. The ancestor of both families was saprophagous and recent species of Anthomyzidae seem to form a transitional stage from phytosaprophagy to phytophagy (Roháček 1998).

Identification

Approximately 55 species in three genera have been described globally. The genus *Scelomyza*, represented by the single species *S. hirticornis* Séguy, 1938, known from Kenya, was considered to belong to the family Opomyzidae by Séguy (1938) and later by Hennig (1972), who studied the type material and was listed as such by Stuckenberg (1980: 635). The genus was later formally transferred to the Anthomyzidae by Roháček (2014) and the family Opomyzidae is now considered to comprise only three genera, *viz*. *Anomalochaeta* (non-Afrotropical), *Geomyza* and *Opomyza*. Brunel (1998) stated that all described species of Opomyzidae occur in the Holarctic Realm and although the majority do, four species were described from the Afrotropics. Opomyzidae are best micropinned in the field for later double-mounting (see Chapter 2).

Key to genera of Afrotropical Opomyzidae

1. Wing extremely narrow (stenopterous), with alula and anal angle markedly reduced (Fig. 8); scutellar disk bare (Fig. 6); scutellum with 4 marginal scutellar setae, the basal 2 shorter (Fig. 6); antennal arista pubescent to dorsally plumose (Fig. 3); 1 or more subvibrissae strong, vibrissa-like (Fig. 3) . . . . . *Geomyza* Fallén

– Wing normally developed, with distinctly produced alula and marked anal angle (Fig. 7); scutellar disk setulose (even if sparsely so) (Fig. 5); scutellum with 4 subequal marginal scutellar setae (Fig. 5); antennal arista pubescent (Fig. 2); subvibrissal setulae all short and fine (Fig. 2). . . . . *Opomyza* Fallén

Synopsis of the fauna

A small family with only four species recognised to date from the Afrotropical Region.

***Geomyza* Fallén.** A genus of 39 described species occurring in the Afrotropical, Nearctic and Palaearctic Regions. Only the single stenopterous species, *G. alluaudi* occurs in the Afrotropics, recorded from Kenya and Tanzania in East Africa (Hendel 1917; Stuckenberg 1980: 635). As a stenopterous opomyzid the species was unfortunately omitted from the "Key to Diptera families—adults" (Chapter 12) by Marshall *et al*. (2017) and the review of flightless Afrotropical Diptera in Chapter 9 (Kirk-Spriggs 2017). The biology and immature stages of the species remain unknown.

***Opomyza* Fallén.** A genus of 15 described species occurring in the Afrotropical, Nearctic and Palaearctic Regions. Three species, *O. australis* Stuckenberg, 1963, *O. capensis* Stuckenberg, 1963 and *O. milleri* Barraclough, 1999, are described from South Africa. Extralimital species of the genus are confined to the Holarctic Realm and currently no plausible hypothesis has been proposed to explain this remarkably disjunct distribution (Barraclough 1999). The biology and immature stages of Afrotropical species remain unknown. An identification key to the three Afrotropical species was provided by Barraclough (1999).

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XENASTEIIDAE 85

(Xenasteiid Flies)

David A. Barraclough

Fig. 85.1. Male of *Xenasteia* sp. (non-Afrotropical) (photograph © S.A. Marshall).

Diagnosis

Very small-sized (body length: 1.3–1.7 mm) acalyptrate flies, scutum pale anteriorly and dark posteriorly (in Afrotropical species), with unusual and reduced wing venation (Fig. 3).

Head with eye clothed in short, erect setulae; postocellar setae minute and convergent; 3 pairs of fronto-orbital setae present (anterior pair inclinate and posterior 2 pairs typically reclinate, other smaller setae present, adjacent to fronto-orbital plate) (Fig. 2); antennal pedicel with prominent dorsal seta; arista bare, or with very short branches; 1 pair long, thin vibrissae; palpus and mouthparts well-developed.

Thorax (setation): postpronotal setae absent; 2 notopleural setae, 1 presutural seta, 1 supra-alar seta, 2 postalar setae, 2 postsutural dorsocentral setae (anterior less than ½ length of posterior), without enlarged prescutellar acrostichal setae, 2 pairs scutellar setae; 1 proepisternal seta; anepisternal setae absent; 1 strong katepisternal seta, often with a weaker seta more anteriorly; preapical dorsal setae lacking on tibiae. Wing (Fig. 3): costal vein (*C*) with subcostal and humeral breaks (latter may be indistinct); subcostal vein (*Sc*) complete to wing margin, although evanescent apically; vein R_{2+3} short; crossvein *r–m* weakly developed, situated near base of radial sector (*Rs*); vein M_1 evanescent past level where veins R_{2+3} and R_{4+5} fork; vein M_4 present, albeit incomplete and thin; anal veins lost; alula well-developed, with fringe of very long marginal setulae.

Abdomen with spiracles in segments 2–6 only (in margins of tergites); both sexes with second sternum divided into 2 narrow plates; first sternite a narrow band; male terminalia distinctive: pair of prominent, posteriorly projecting lobes on posterior margin of hypandrium, each with 2 spine-like setulae (Fig. 4); phallus highly reduced and inconspicuous, mostly membranous; female cerci small and free.

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2021. Manual of Afrotropical Diptera. Volume 3. Brachycera—Cyclorrhapha, excluding Calyptratae. *Suricata* 8. South African National Biodiversity Institute, Pretoria; pp. 1909–1911.

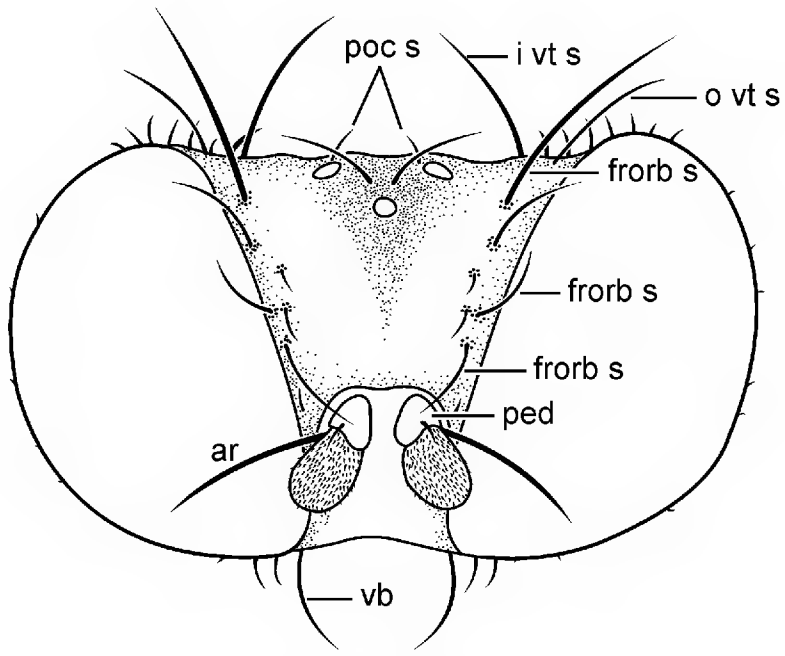
Xenasteiidae may superficially resemble some species of Asteiidae (see Chapter 92), but are immediately distinguished by the weak convergent postocellar setae (if present, stronger and parallel, or divergent in Asteiidae), the presence of anterior fronto-orbital setae and two costal breaks (breaks entirely lacking in Asteiidae).

Biology and immature stages

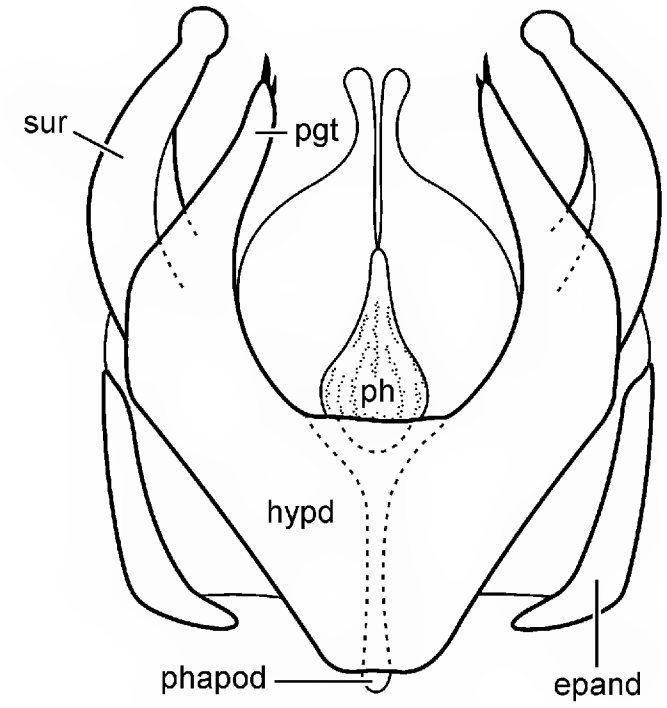
Virtually nothing is known regarding the biology and phenology of the two Afrotropical species, *Xenasteia aldabrae* and *X. seychellensis*, both of which were described by D.E. Hardy in 1980. *Xenasteia aldabrae* has, however, been recorded at light traps on the atoll of Aldabra. Elsewhere, *Xenasteia* Hardy species appear to be associated with xeric, sandy habitats, particularly seashores (Grimaldi 2009). They have been found on decaying fish on an Indian Ocean island and on *Pandanus* (Pandanaceae) leaves (Grimaldi 2009; Hardy 1980; Ismay 2003). *Tunisimyia* Papp, the second xenasteiid genus, distributed across Mediterranean shores, has been collected from *Tamarix* (Tamaricaceae) trees (often in bloom) (Carles-Tolrá 1995; Freidberg 1994; Grimaldi 2009), *Crithmum maritimum* L. (Apiaceae) stems (Grimaldi 2009; Papp 1980) and *Sesuvium portulacastrum* L. (Aizoaceae) (Marshall 2012: 369), all being plants associated with coastal habitats. The immature stages are undescribed.

Economic significance

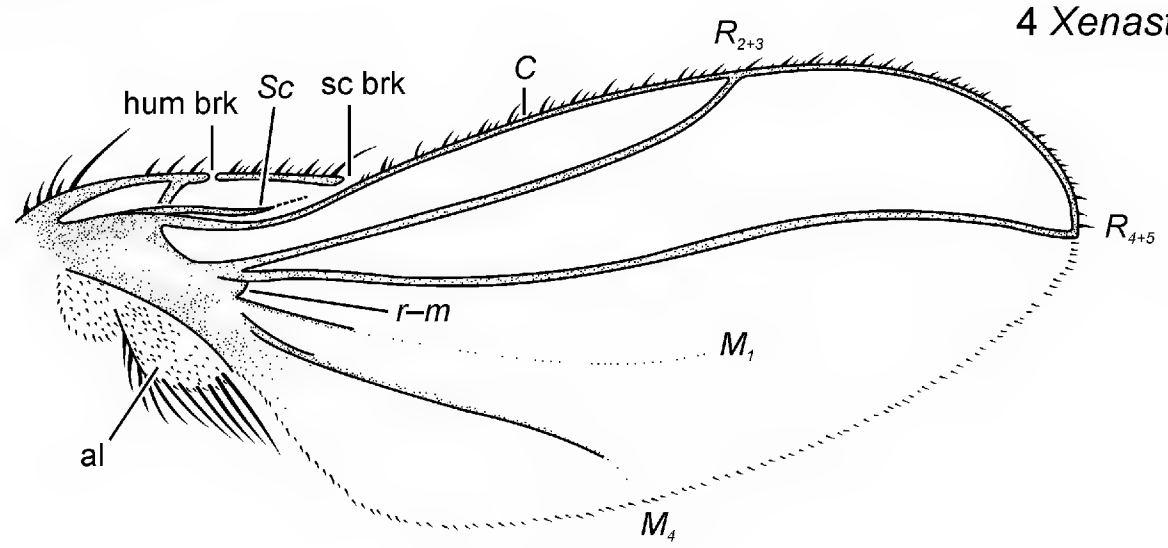
Xenasteiidae have no known economic significance.



2 *Xenasteia*



4 *Xenasteia*



3 *Xenasteia*

Figs 85.2–4. Head, wing and male terminalia of Xenasteiidae: (2) head of *Xenasteia similis* Hardy, dorsal view (non-Afrotropical); (3) wing of *X. sabroskyi* Hardy, dorsal view (non-Afrotropical); (4) male terminalia of *X. aldabrae* Hardy, ventral view. Figs 2–4 (after Hardy 1980, figs 7a, 5a, 1a, respectively).

Abbreviations: al – alula; ar – arista; C – costal vein; epand – epandrium; frorb s – fronto-orbital seta; hum brk – humeral break; hypd – hypandrium; i vt s – inner vertical seta; M_1 – first branch of media; M_4 – fourth branch of media; o vt s – outer vertical seta; ped – pedicel; pgt – postgonite; ph – phallus; phapod – phallapodeme; poc s – postocellar setae; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Sc* – subcostal vein; sc brk – subcostal break; sur – surstylus; vb – vibrissa.

Classification

The family has received limited attention since its description in 1980. Papp (1998: 307) considers that the various morphological reductions, such as the reduced wing venation, make assessing phylogenetic relationships problematic. McAlpine (1989: 1466) (also Yeates *et al*. (2007)) placed the Xenasteiidae in the superfamily Opomyzoidea, within the suprafamily Asteoinea, together with the Asteiidae, Aulacigastridae, Neurochaetidae, Periscelididae and Teratomyzidae (non-Afrotropical). This suprafamily classification was also followed by Grimaldi (2009). Pape *et al*. (2011) placed the family in a possibly paraphyletic Opomyzoidea. It is important to note that Tunisimyiidae has been synonymised with Xenasteiidae (see McAlpine 1989: 116).

Identification

Hardy (1980) included the two recorded Afrotropical species of *Xenasteia* in an identification key to species of Xenasteiidae known at that time. All three Indian Ocean island species (the two Afrotropical species, plus *X. similis* Hardy, 1980 from Diego Garcia Is.), have a characteristic bicolourous scutum. This character, together with Hardy's description and illustration of the male terminalia, should facilitate future identification of the named Afrotropical species. Xenasteiidae are best micro-pinned in the field for later double-mounting (see Chapter 2).

There is a possibility that *Tunisimyia* may fringe into the northern part of the Afrotropical Region. It is immediately distinguished from *Xenasteia* by the presence of crossvein *r–m* and two katepisternal setae (only one in *Xenasteia*).

Synopsis of the fauna

***Xenasteia* Hardy.** A genus of 11 described species occurring in the Afrotropical, Australasian and Oriental Regions. Xenasteiidae have only been recorded from islands in the south-easterly fringes of the Afrotropical Region: Mahé Is. and the coral atoll of Aldabra, which is 1,150 km to the south-west of Mahé and 426 km north-west of Madagascar (both islands form part of Seychelles). The genus was also recently sampled in coastal and indigenous forest habitats in the east of Réunion Is. (A.H. Kirk-Spriggs, pers. comm. 2017). Somewhat surprisingly, the family has not yet been collected from Madagascar or the coast of East Africa. Only the genus *Xenasteia*, occurs in the Afrotropical Region. *Tunisimyia*, is known only from two species from the shores of the Mediterranean (Israel, Spain and Tunisia), while some 11 species of *Xenasteia* are recorded from scattered Indo-Pacific islands, from Hawaii and Fiji in the east through New Guinea, to as far west as Aldabra. The range extends as far north as Okinawa (south of Japan) and Taiwan (Papp 2005).

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Papp, L. 1998. 3.25. Family Xenasteiidae. *In*: Papp, L. & Darvas, B., eds, *Contributions to a manual of Palaearctic Diptera (with special reference to flies of economic importance). Volume 3. Higher Brachycera*. Budapest: Science Herald, Budapest, pp. 305–308.

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AGROMYZIDAE 86

(Leaf-mining Flies)

Owen Lonsdale and Michael von Tschirnhaus

Fig. 86.1. Female of *Phytomyza* (*Phytomyza*) sp. (non-Afrotropical) (photograph © S.A. Marshall).

Diagnosis

Small- to medium-sized acalyptrate flies (wing length: 1.5–3.5 mm, sometimes as small or as large as 0.5 mm and 6.5 mm, respectively), often short and compact, but sometimes narrow; females with stout, conspicuous oviscape (Figs 1, 2); colour variable, from black to yellow (Figs 2, 3), or patterned; dark species sometimes with metallic sheen (many *Melanagromyza* Hendel, but also some *Japanagromyza* Sasakawa and *Ophiomyia* Braschnikov); sometimes with grey (Fig. 1) or brownish pruinosity.

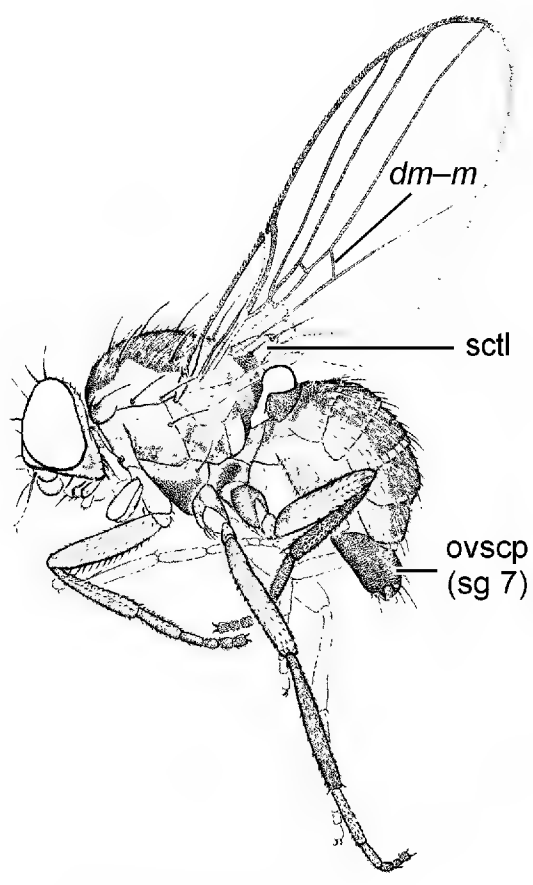
Head with antenna porrect; arista dorsobasal, usually pubescent (Figs 6–10), sometimes short to long plumose; compound eye bare (Fig. 7), or with microtrichia (Fig. 6), without metallic sheen; lunule distinct, sometimes large (Fig. 7); frons usually bare (setulae sometimes present above lunule), soft medially, sometimes well-sclerotised; ocellar triangle variably sclerotised, restricted to ocellar tubercle to very large, sometimes reaching lunule; parafacial running as "cheek" along face and beneath eye, sometimes well-separated from ventral section of gena ("jowl") by "genal groove" (Fig. 7); proboscis normal, sometimes elongate; palpus normally narrow, finger-like, rarely enlarged or swollen; usually 4 fronto-orbitals, rarely less than 3, sometimes 5 or more; historically divided into anterior inclinate "inferior fronto-orbital setae" and posterior reclinate/inclinate "superior fronto-orbital setae"; usually 1 or 2 rows of orbital setulae, sometimes absent or in several rows, reclinate to upright (Figs 6–8, 10) or proclinate (Fig. 9); postocellar and ocellar setae usually well-developed (e.g., Fig. 8), invariably diverging, postocellar rarely absent; 1 inner and 1 outer vertical seta (Figs 6–10); one vibrissa, sometimes small, sometimes

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2021. Manual of Afrotropical Diptera. Volume 3. Brachycera—Cyclorrhapha, excluding Calyptratae. *Suricata* 8. South African National Biodiversity Institute, Pretoria; pp. 1913–1938.

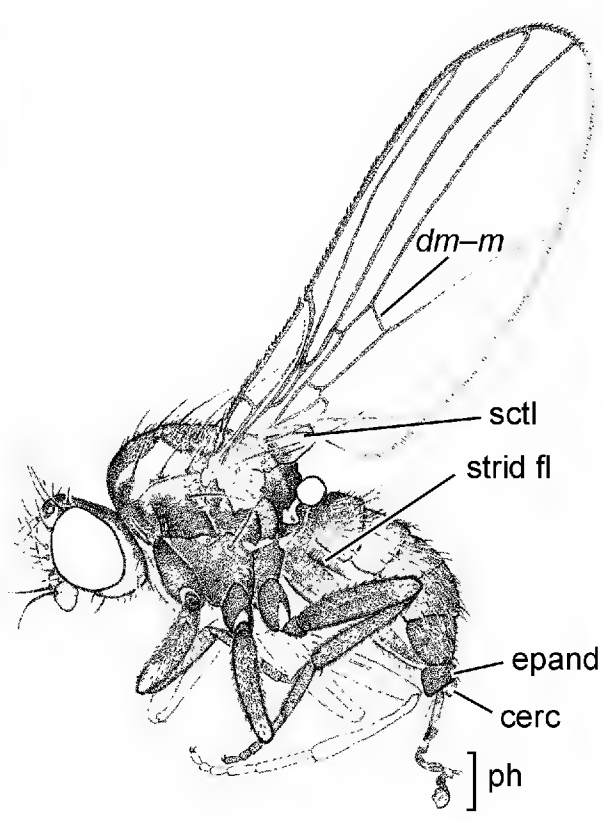
duplicated or multiplicated, fused into pointed "fasciculus" or "horn" in male *Ophiomyia* (Fig. 8).

Thorax without precoxal and postmetacoxal bridges; 1 postpronotal seta; 2 (exceptionally 1) notopleural setae; 2–4 dorsocentral setae, but sometimes up to 7, sometimes decreasing in size anteriorly; prescutellar acrostichal seta sometimes present; acrostichal setulae usually in 4–10 rows at level of transverse suture, sometimes more, sometimes entirely absent or reduced to a few setulae; presutural and postsutural supra-alar setae in row with postalar setae; 1 postsutural intra-alar seta usually present; exterior postalar seta present, interior postalar seta rarely absent; 1 proepimeral seta (rarely absent); at least 1 anepisternal and 1 katepisternal seta. Scutellum with 1 apical marginal scutellar seta, usually 1 anterolateral scutellar seta (absent in two subgenera of *Cerodontha* Rondani); scutellum disk otherwise bare, but a few species with several scattered tiny setulae, and Palaearctic *Selachops* Wahlberg with scutellum disk densely clothed in setulae. Wing well-developed, membrane usually unpigmented, but exceptionally whitish, clouded or pictured, veins usually dark to yellowish; vein M_1 in some genera weak or faded (Figs 15, 16, 18); costal vein (C) reaching vein R_{4+5} or vein M_1; subcostal break present, humeral break absent; subcostal vein attaining costal vein (sometimes as a fold) (Figs 13–18), or fused to vein R_1 apically (Figs 11, 12); vein R_1 bare (some *Phytobia* Lioy with some setulae); apex of vein R_1 sinuous if subcostal vein complete; cell *cua* (anal cell) present (Fig. 12); crossveins *r–m* and *dm–m* present (Figs 11–15) or absent (Figs 16–18); crossvein *bm–m* rarely absent (some *Pseudonapomyza* Hendel); vein *CuA+CuP* never reaching wing margin; halter white, yellow, black or bicoloured. Legs with at least mid tibia usually with small ventroapical seta; sometimes mid tibia, or fore and mid tibiae with medial posterolateral seta/e.

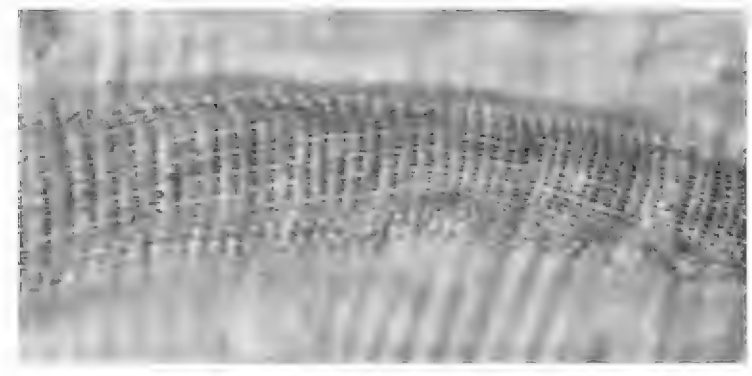
Abdominal tergites and sternites well-developed; tergites 1 and 2 fused; sternites narrower, less setose; male abdomen with sternite 5 large, with broad, deep posteromedial emargination; sternites 6–8 atrophied, usually only present as narrow, dorsal sclerotised band; epandrium and surstylus (Figs 19–21) often relatively small, sometimes fused; cercus (1 pair) usually simple, linear, sometimes enlarged and/or with tubercle-like setae or spinules (Figs 19–21); subepandrial sclerite sometimes expanded into lobe ventrally ("Langfortsatz" *sensu* Nowakowski 1973; *Cerodontha* and some *Liriomyza* Mik); hypandrium U- to V-shaped, sometimes with strong distomedial apodeme; postgonite usually long and narrow with one seta; pregonite absent; phallus usually elaborate, segmented, consisting of basiphallus (usually comprising one or two plates flanking ejaculatory duct and separate basal ring termed "phallophorus"), mesophallus and distiphallus, sometimes variably fused or further subdivided (Figs 24, 25, 27, 54); paraphallus (1 pair, lateral) and hypophallus (ventral) sometimes present distal to basiphallus; segmented epiphallus surrounding base of phallus and phallapodeme, and articulating with postgonite; ejaculatory apodeme (Fig. 26) sclerotised, size reduced to very large and heavily sclerotised; female abdomen with tergite and sternite 7 fused to form dark, heavily sclerotised, non-retractile oviscape, with anterodorsal apodeme projecting into abdomen (Figs 2, 57, 58); remaining apical segments telescoped within oviscape; membrane between segments 7 and 8 with



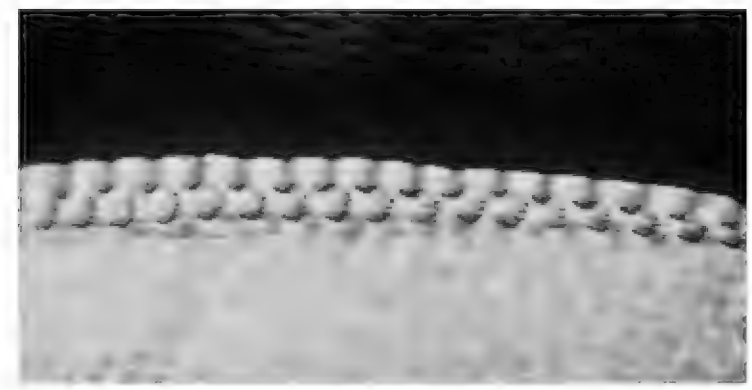
2 *Liriomyza* ♀



3 *Liriomyza* ♂



4 *Liriomyza*



5 *Agromyza*

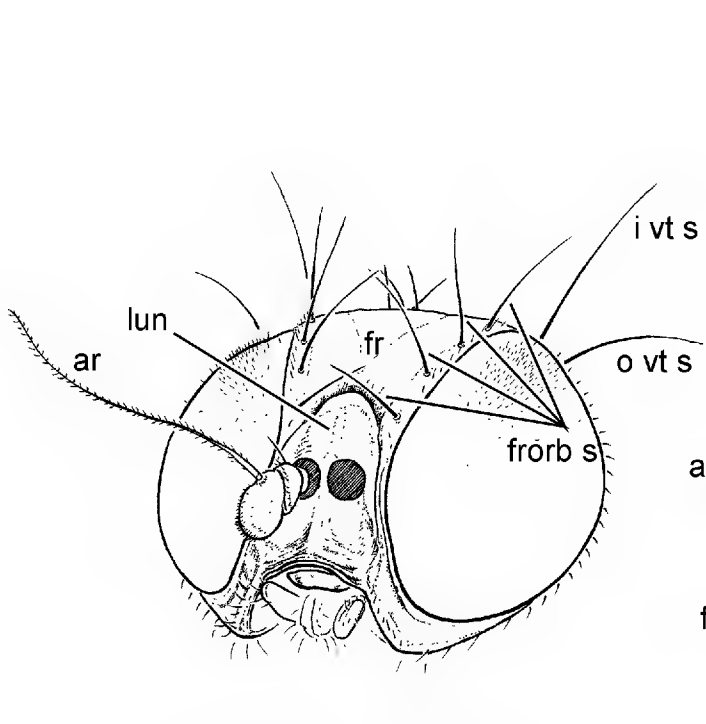
Figs 86.2–5. Habitus and stridulatory files of Agromyzidae: (2) habitus of *Liriomyza sativae* Blanchard, lateral view ♀; (3) same, *L. septentrionalis* Sehgal (non-Afrotropical) ♂; (4) stridulatory file in membrane of *Liriomyza* sp., lateral view; (5) same, along margin of syntergite 1 + 2 in *Agromyza* sp. Figs 2, 3 (Lonsdale 2011, figs 1, 2).

Abbreviations: cerc – cercus; *dm–m* – discal medial crossvein; epand – epandrium; ovscp – oviscape; ph – phallus; sctl – scutellum; sg – segment; strid fl – stridulatory file.

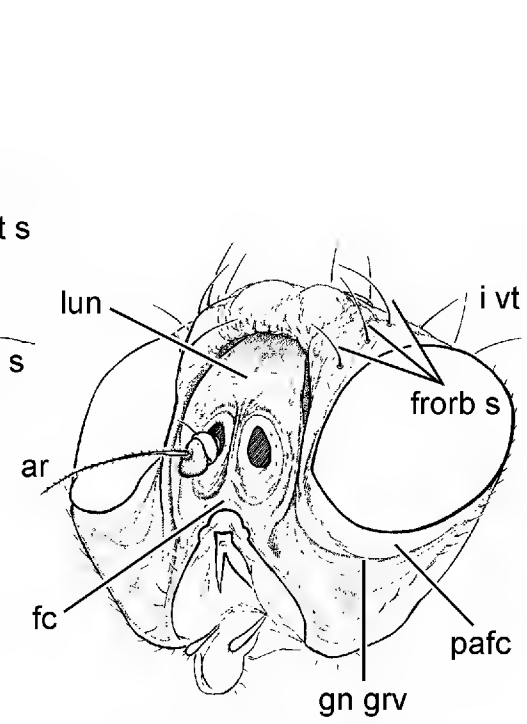
2 pairs of sclerotised fascia (Figs 57, 58), dorsal and ventral membrane beyond segment 8 densely covered with pattern of anteriorly directed denticles (Fig. 64) (for drilling into plant epidermis); 1 pair of species-specific sclerotised egg-guides sometimes present, partly with denticles and serrate edges, interpreted as derivates of sternite 8 (used for scraping out hole for egg positioning); 1 pair of separate cerci with normal or stiff apical setae (Figs 59–63) (partly adapted as piercing mechanism in seed-feeders); ventral receptacle and spermatheca (1 pair) usually small and sclerotised (Figs 65–68).

Egg small, clear and ovate to reniform; surface smooth to reticulate; end bearing small micropyle often broader (Ferrar 1987: 61).

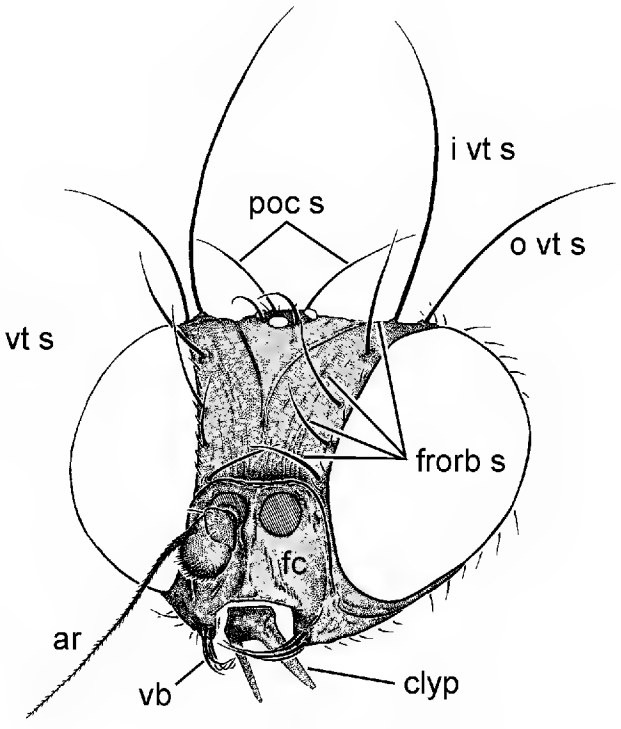
Larva thoroughly treated by Dempewolf (2001) and Ferrar (1987: 61), generally uniform in appearance, being soft, cylindrical, tapered at both ends, typically maggot-like (Figs 69, 70); form varying little between leaf-mining, stem-boring and gall-inducing species (Dempewolf 2005: 410); body size small, length usually ranging from 1.5–3.0 mm, with *Phytobia* species often longer and narrower (Spencer 1987: 870), sometimes reaching length of 20 mm (Martinez *et al*. 1985; Moraal & Grijpma 1987); cephaloskeleton (Figs 71–73) with mouthhooks often asymmetrical, firmly fused basally, moving in same direction (Spencer 1987: 870) (allowing for thinner, cleaner mines within specific leaf layers without breaking leaf surface); sometimes only 1 or 2 accessory teeth on each mouthhook, that may be duplicated and variable in shape, often becoming



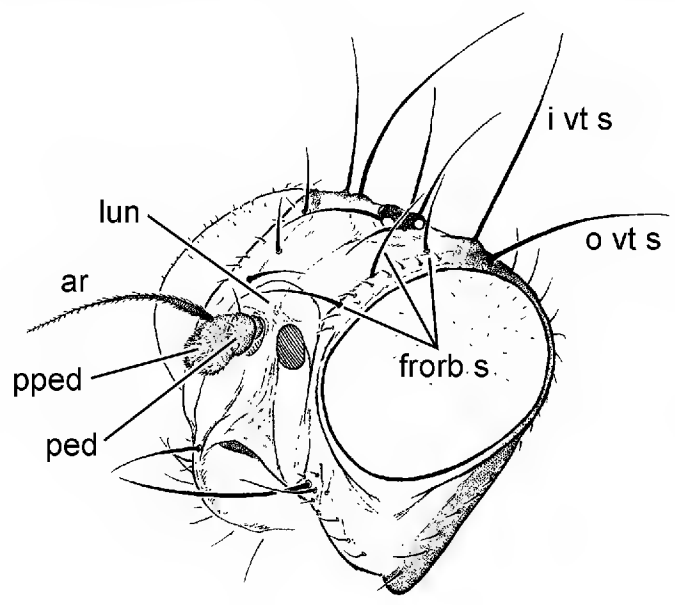
6 *Melanagromyza*



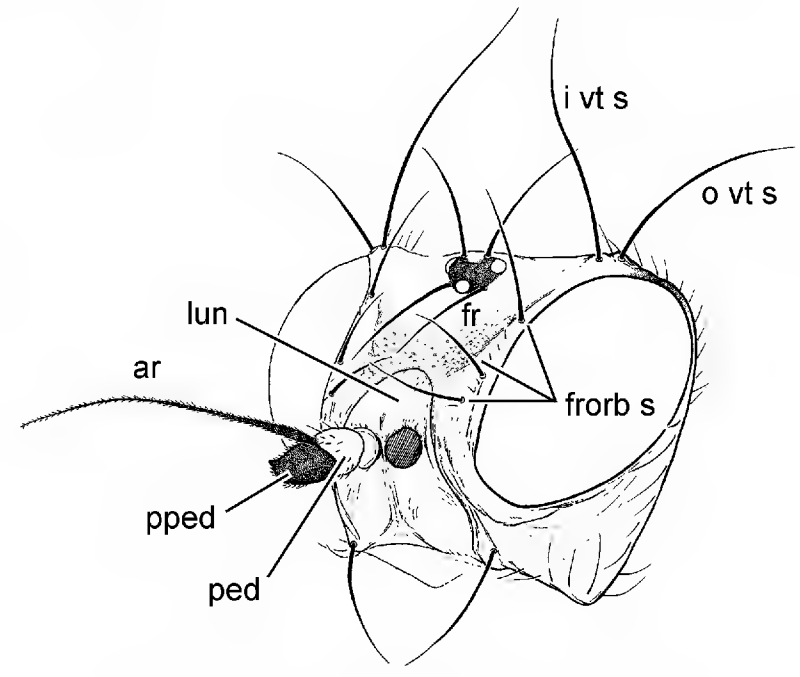
7 *Ophiomyia*



8 *Ophiomyia*



9 *Phytomyza* (*Phytomyza*)



10 *Cerodontha* (*Cerodontha*)

Figs 86.6–10. Heads of Agromyzidae (anterolateral views): (6) *Melanagromyza metallica* (Thomson); (7) *Ophiomyia aloes* (Spencer); (8) *Ophiomyia* sp.; (9) *Phytomyza* (*Phytomyza*) *horticola* Goureau; (10) *Cerodontha* (*Cerodontha*) sp. Figs 6–8 (Lonsdale 2014, figs 10, 6, 9, respectively).

Abbreviations: ar – arista; clyp – clypeus; fc – face; fr – frons; frorb s – fronto-orbital setae; gn grv – genal groove; i vt s – inner vertical seta; lun – lunule; o vt s – outer vertical seta; pafc – parafacial; ped – pedicel; poc s – postocellar seta; pped – postpedicel; vb – vibrissae.

reduced posteriorly and strengthened in boring species (Dempewolf 2005: 412); intermediate sclerite short; basal sclerite with pair of cornua; Agromyzinae with dorsal, sometimes ventral cornua of basal sclerite encompassing small "window", open posteriorly in dorsal cornu (Fig. 71); Phytomyzinae (Figs 72, 73) sometimes with "window" in ventral cornu only (Spencer 1987: 870); prothoracic spiracles positioned dorsally; larval and puparial spiracles often significant in species identification and taxonomy (Figs 79–81); prothoracic and posterior spiracles with at least 3 or 5 slit-like spiracular openings (respectively) in clusters of papillae/bulbs that may be narrow and reduced or strongly projecting and expanded (especially in species using spiracles to anchor puparium to host-plant surface); prothoracic spiracles closely spaced, not projecting in first-instar larva (Ferrar 1987: 62).

Puparium smooth, shiny; colour sometimes white, but more often pale yellow to dark orange (Figs 74–76), with some, including overwintering puparia, dark brown to black; shape slender to more compact, barrel-shaped; segmentation sometimes evident, minute sculpturing or pits sometimes present; adult eclosion from puparium typical of other Schizophora (Fig. 77), but in *Ophiomyia* genus-group, puparial cap with additional fissure along midline (Fig. 78) (Dempewolf 2001).

Adult Agromyzidae may be superficially confused with Chloropidae (see Chapter 96) because of their small size, colouration and sometimes enlarged ocellar triangle, but Chloropidae lack an anal cell and stout oviscape, and they have a vertical propleural carina. Other families with a conspicuous oviscape, such as those in the superfamily Tephritoidea, lack a vibrissa and usually have conspicuously patterned wings. Similar chaetotaxy is seen in some Odiniidae (see Chapter 83) and Clusiidae (see Chapter 81), but these lack the oviscape, and most have preapical tibial setae; some Clusiidae do not have these tibial setae, but all have a projection on the outer distal surface of the pedicel. Fergusoninidae (non-Afrotropical) are bright yellow species with an anteriorly flattened head with a small ventral face and antenna and a large parafacial and lunule. Some Milichiidae (see Chapter 95) can be similar in habitus, but these have convergent postocellars.

Biology and immature stages

The larvae of all Agromyzidae feed in the living tissue of plants, including monocotyledons, dicotyledons, horsetails, ferns and liverworts (Hering 1957, 1966; Spencer 1990: xi); no species are known from thallophytes, mosses, Lycopsida, Ephedraceae or conifer foliage. Numerous species mine in leaves (Figs 84–86), but some also mine/bore in roots, twigs (Fig. 83), trunks (Figs 87, 88), flower heads, seed pods and single seeds and some species induce galls (Fig. 82). The immature stages of stem- and trunk-mining species can be difficult to locate, making host data relatively sparse for these taxa, but leaf-miners are relatively easy to find, as their pale mines can be spotted from a distance and data for these species are subsequently much more abundant.

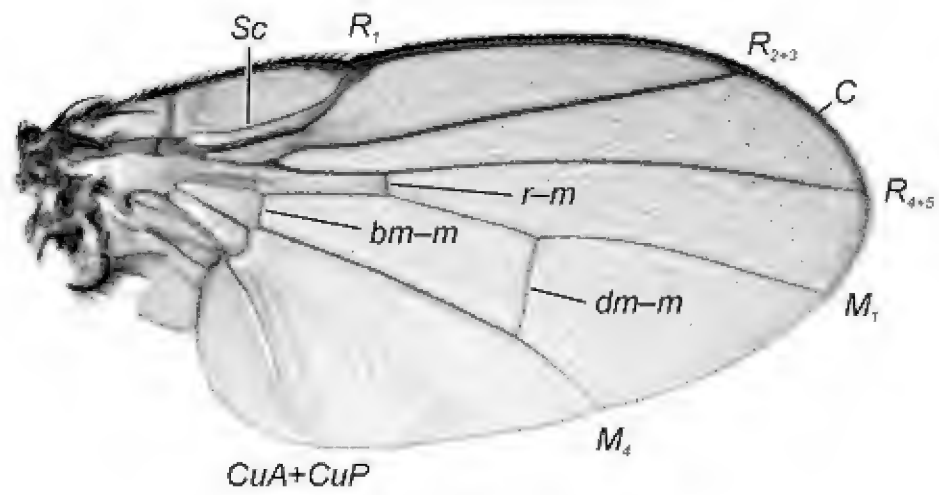
Probably exclusively among all Diptera leaf-miners, larvae are found moving and feeding on their side, alternatively right and left, sweeping their body dorsoventrally to shave-off and ingest sections of the cell layer in a process discussed in Dempewolf (2005: 412). Host usage and damage are often characteristic for species, with taxa presenting specific frass depositions within characteristically shaped mines that vary from linear to blotch or compact spirals and are sometimes restricted to particular cell layer/s within the leaf, or a particular section of the leaf, such as the margin or midrib (Dempewolf 2005: 408; Ferrar 1987: 60). *Phytobia* species occur beneath the bark of dicotyledons or rarely gymnosperm trees, producing characteristic "pith flecks" (= medullary spots), while feeding on young xylem (Fig. 88), tissue incorrectly referred to in the past as "cambium" (see discussion in Ylioja *et al*. 1998). A number of stem-borers across numerous genera also characteristically induce galls in the host tissue (Fig. 82), discussed in detail by Dempewolf (2005: 418). Two species are known to mine in the galls of other insects – a weevil (Coleoptera: Curculionidae) in Europe (Kock 1966) and an ant (Hymenoptera: Formicidae) in the Afrotropics (Hocking 1971; Spencer 1963*a*). A minority of taxa switch between leaf and stem mining (as in *Ophiomyia phaseoli* (Tryon, 1895)), or stem and seed consuming (as in the Palaearctic *Phytoliriomyza ornata* (Meigen, 1830) and many *Phytomyza* Fallén (*Napomyza* Westwood)), and for some, feeding traces or cell layers utilised may alter with host species, larval stage or seasonality (Dempewolf 2005: 408; Lonsdale & Scheffer 2011; Nowakowski 1962).

Oviposition is accomplished through insertion of the ovipositor into plant tissue below or within the epidermis, following initial puncture by the saw-like action of the egg-guides (when present). This puncturing and oviposition may sometimes cause severe damage to the plant in high densities. Larvae emerge within several days after oviposition to begin feeding by digging a mine or channel through the host (Spencer 1987: 871). Adult females predominantly feed through puncturing of the host-plant with their ovipositor, with intake of the exuding leaf sap, sometimes with one to two hundred punctures produced serially; males may also feed from these punctures (Aukema *et al*. 1996; Ferrar 1987: 61). In electrolyte-poor tropical forests, males are attracted in great numbers to sweat, urine or other salt-containing fluids, which they suck until the abdomen is greatly swollen (Tschirnhaus 1991).

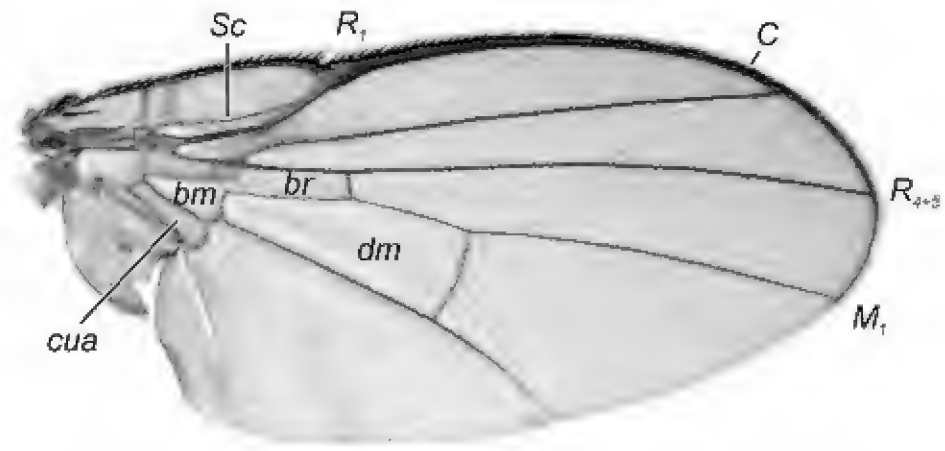
Depending on the species, larval feeding may range from the period of a single week to up to 10 months and may vary within species, depending on host and temperature (USDA 2008). Feeding period also depends on voltinism, as species with multiple generations per year have more rapid development and on life cycle, as long-overwintering (and presumably also drought avoiding) larval stages involving occasional feeding will only advance to later stages with the return of favourable conditions (Spencer 1987: 871).

Pupariation takes place either in the soil, or in/on the host-plant; duration is quite variable and often associated with overwintering or (presumably) aestivation or obligatory diapause. Some true winter miners with larval diapause in the summer are also known. If partially emerged, puparia will be partially fastened inside the mine, usually by spiracula penetrating the plant epidermis or cement-like frass (e.g., gall producers and some *Calycomyza* Hendel), but uncommonly also by strong silky threads; if entirely emerged, puparia are fastened to the plant *via* enlarged spiracles or hardened larval excrement.

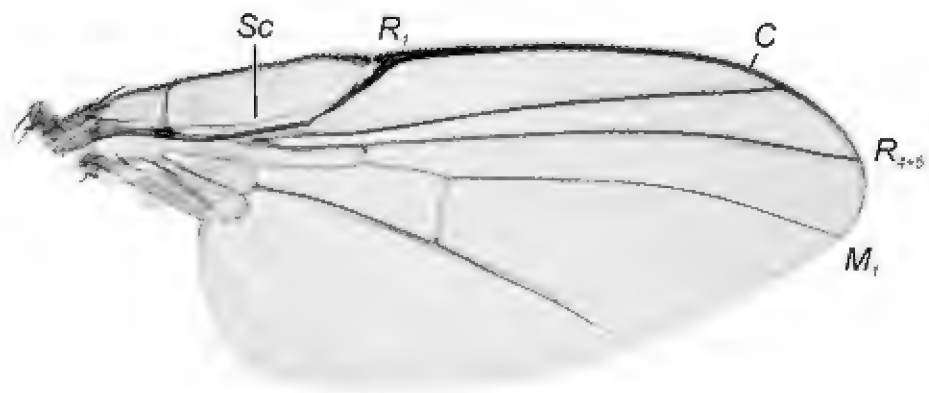
Hosts are known for approximately half of all valid species, based on observations mainly from the Palaearctic, but also



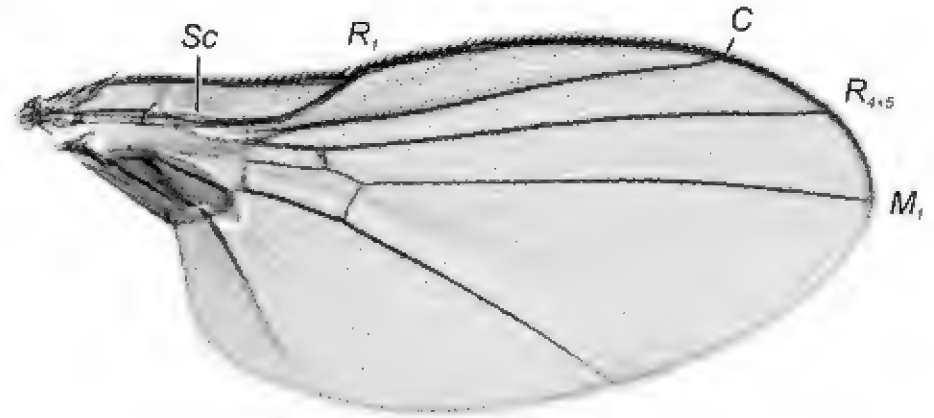
11 *Agromyza*



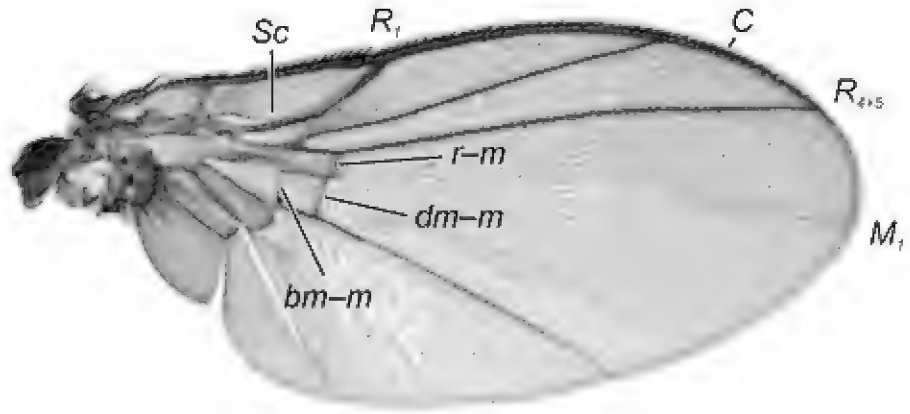
12 *Melanagromyza*



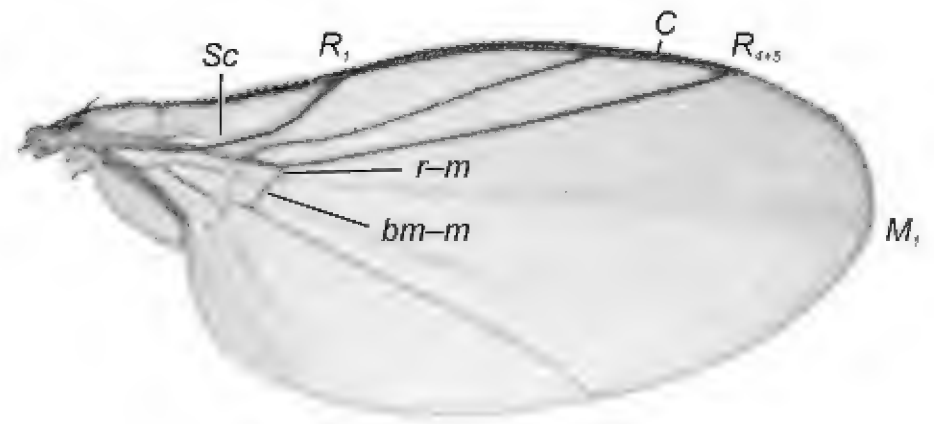
13 *Phytobia*



14 *Amauromyza*



15 *Pseudonapomyza*



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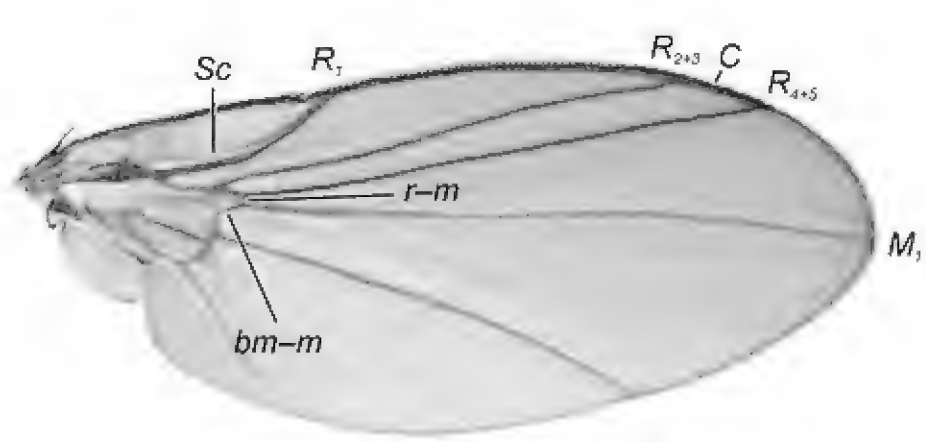
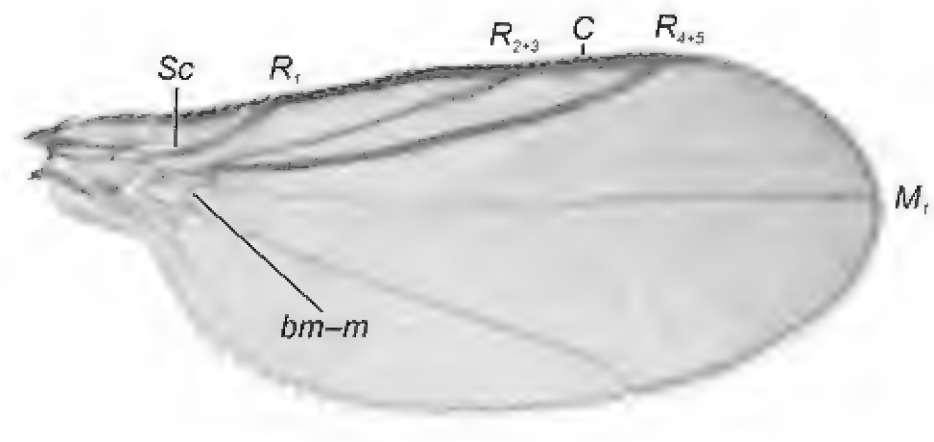


17 *Phytomyza* (*Phytomyza*)



18 *Phytomyza* (*Ptochomyza*)

Figs 86.11–18. Wings of Agromyzidae (dorsal views): (11) *Agromyza* sp.; (12) *Melanagromyza metallica* (Thomson); (13) *Phytobia setosa* (Loew); (14) *Amauromyza flavifrons* (Meigen) (non-Afrotropical); (15) *Pseudonapomyza* sp.; (16) *Ps. atra* (Meigen); (17) *Phytomyza* (*Phytomyza*) *horticola* Goureau; (18) *Ph.* (*Ptochomyza*) *asparagi* (Hering) (non-Afrotropical).

Abbreviations: *bm* – basal medial cell; *bm–m* – basal medial crossvein; *br* – basal radial cell; *C* – costal vein; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *dm* – discal medial cell; *dm–m* – discal medial crossvein; M_1 – first branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Sc* – subcostal vein.

some North American researchers. A comprehensive list of references to these works was accumulated by Spencer (1990: 408), who provided the most significant compilation of host records for the family, later to be expanded by Benavent-Corai *et al*. (2005).

Many Agromyzidae are believed to feed on only a single species of plant (Spencer 1990: xii), but this may be an artefact of incomplete rearing records, with recent data suggesting that at least some of the flies once considered to be restricted to a single host may in fact be able to mine in several related species or genera (Lonsdale & Scheffer 2011). Monophagy in the wider sense, encompassing hosts in single genus- or family-level groups, is more likely to be typical of agromyzid species. Emerging support for co-speciation of flies with host-plants is developing for several species-groups, mostly in the genus *Phytomyza* (Scheffer & Hawthorne 2007; Scheffer & Wiegmann 2000), but is also evident in other genera, including specialised species-groups in *Agromyza* Fallén (Griffiths 1963), *Liriomyza* (Lonsdale 2011), *Amauromyza* Hendel and *Cerodontha* (Spencer 1990: 390). Across these specialised groups there is a growing body of evidence that major shifts to different plant families, or other higher taxa, followed by bursts of speciation may occur periodically within lineages (Griffiths 1980; Scheffer & Wiegmann 2000), contrasting the stricter host group fidelity suggested by previous authors.

Polyphagy across plant families is uncommon in the Agromyzidae, being present in only an estimated 16 species (Spencer 1990: 381). These species are often major plant pests, occurring on many agriculturally significant crops, accumulating population size in weeds or other nearby plant species and often readily dispersing to other countries through trade. These mostly include *Liriomyza* species, such as *L. sativae* Blanchard, 1938,

19 *Phytomyza* (*Phytomyza*) ♂

20 *Phytomyza* (*Phytomyza*) ♂

21 *Phytomyza* (*Phytomyza*) ♂

22 *Phytomyza* (*Phytomyza*) ♂

24 *Phytomyza* (*Phytomyza*) ♂

23 *Phytomyza* (*Phytomyza*) ♂

25 *Phytomyza* (*Phytomyza*) ♂

26 *Phytomyza* (*Phytomyza*) ♂

Figs 86.19–26. Male terminalia of Agromyzidae (Phytomyzinae): (19) external terminalia of *Phytomyza* (*Phytomyza*) *horticola* Goureau, posterior view; (20) same, anterior view; (21) same, lateral view; (22) same, internal terminalia (excluding phallus), lateral view; (23) same, ventral view; (24) phallus, lateral view (inset: detail of apex); (25) same, ventral view; (26) ejaculatory apodeme, lateral view.

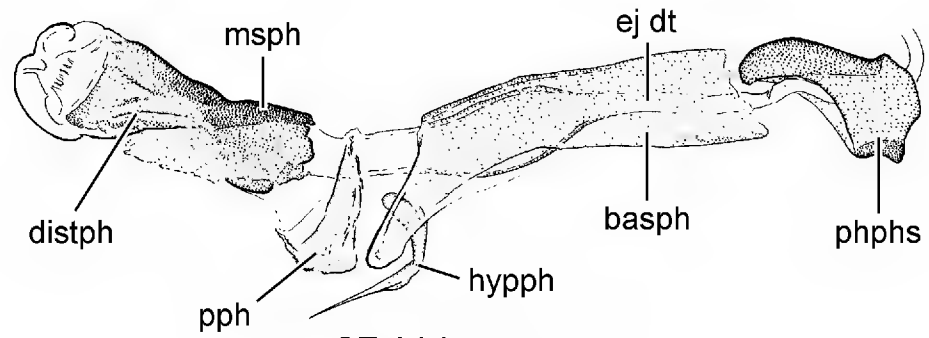
Abbreviations: basph – basiphallus; bl – blade; cerc – cercus; distph – distiphallus; epand – epandrium; epph – epiphallus; hypd – hypandrium; hypph – hypophallus; pgt – postgonite; phapod – phallapodeme; phphs – phallophorus; sbepand scl – subepandrial sclerite; spm pmp – sperm-pump; stm – stem; sur – surstylus.

L. trifolii (Burgess, 1880), *L. bryoniae* (Kaltenbach, 1858), *L. huidobrensis* (Blanchard, 1926) and *L. strigata* (Meigen,1830), the last three mentioned of which are closely related. Lists of host genera and references are available in Benavent-Corai *et al.* (2005) and Lonsdale (2011). Additional widespread polyphages include *Phytomyza* (*Phytomyza*) *horticola* Goureau, 1851, *P.* (*P.*) *syngenesiae* (Hardy, 1849) and several *Tropicomyia* Spencer species (Spencer 1973: 11).

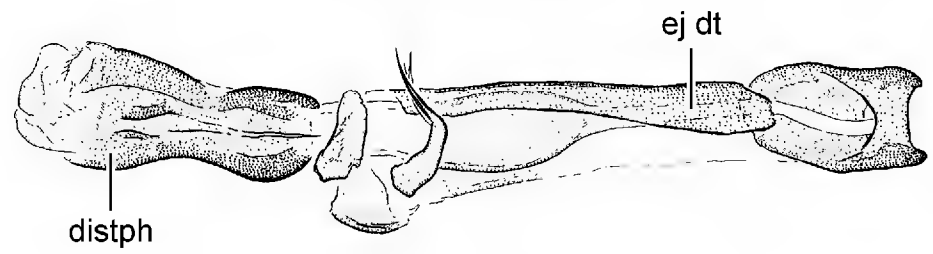
Economic significance

Numerous species of agricultural significance occurring in the Afrotropical Region represent introductions from Europe and North America through trade, likely through the import of infested host-plants or seeds. *Ophiomyia phaseoli* and *Tropicomyia flacourthiae* (Séguy, 1951) are, however, two frequently encountered agromyzine pests native to the Old World tropics.

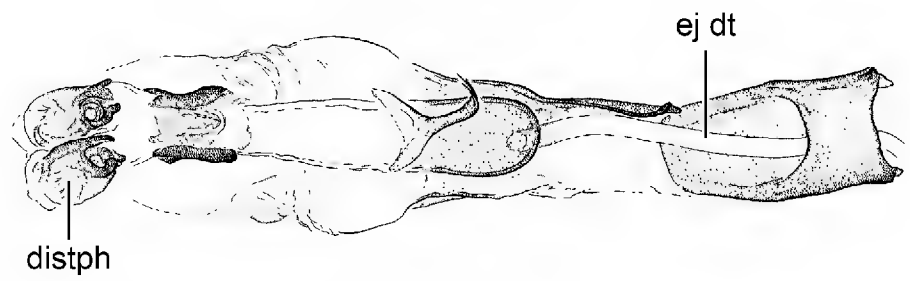
The most significant imported pests from North America belong to the subfamily Phytomyzinae. These are polyphagous leaf-miners in the genus *Liriomyza* (Figs 2, 3), including *L. sativae* (Figs 29, 30), *L. brassicae* (Riley, 1884) (primarily crucifers and peas) (Figs 27, 28) and *L. trifolii* (Figs 33, 34). These *Liriomyza*, which were recently re-described by Lonsdale (2011), with an updated list of host genera, occur on many food crops in sub-Saharan Africa and populations regularly reach pestiferous levels. Another recent pest of global concern is *L. huidobrensis* (Figs 31, 32), which was only known from South America until the 1980s, when populations were found



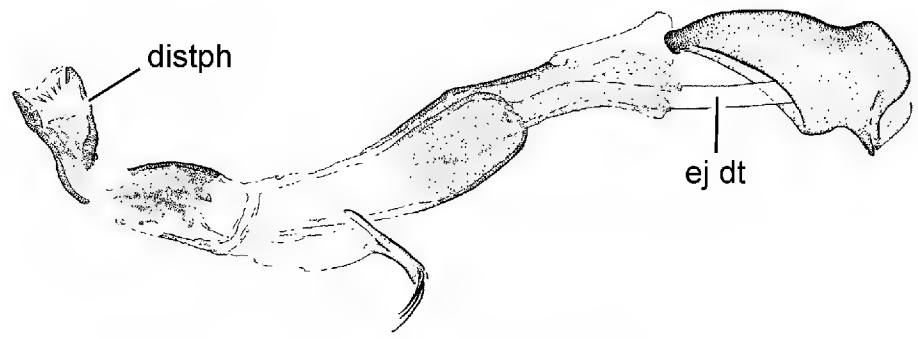
27 *Liriomyza* ♂



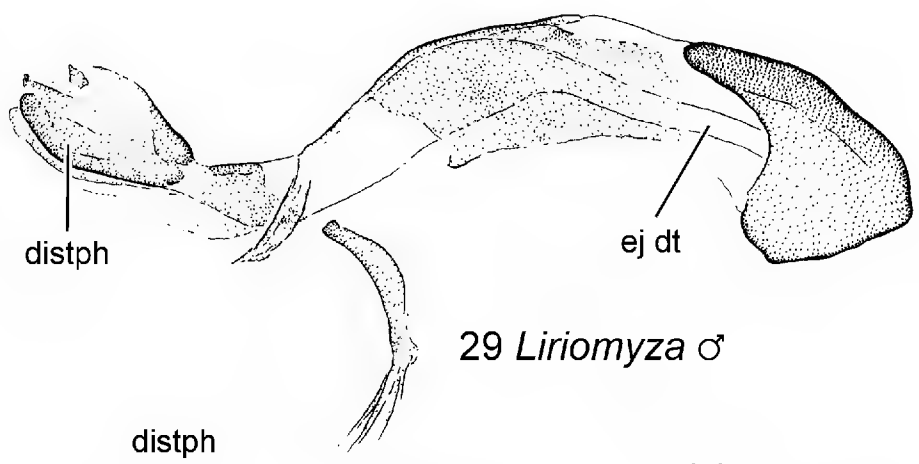
28 *Liriomyza* ♂



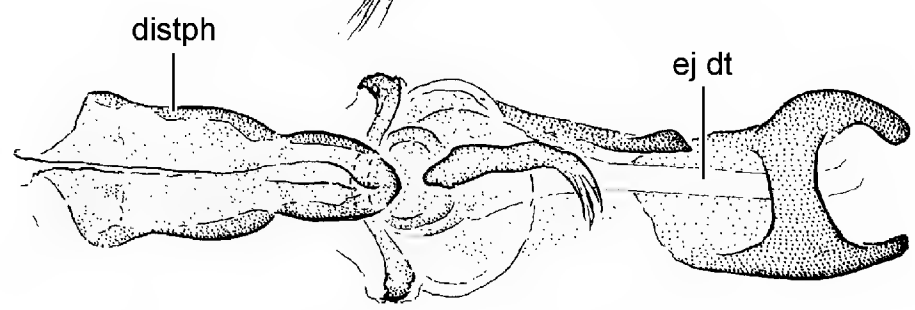
31 *Liriomyza* ♂



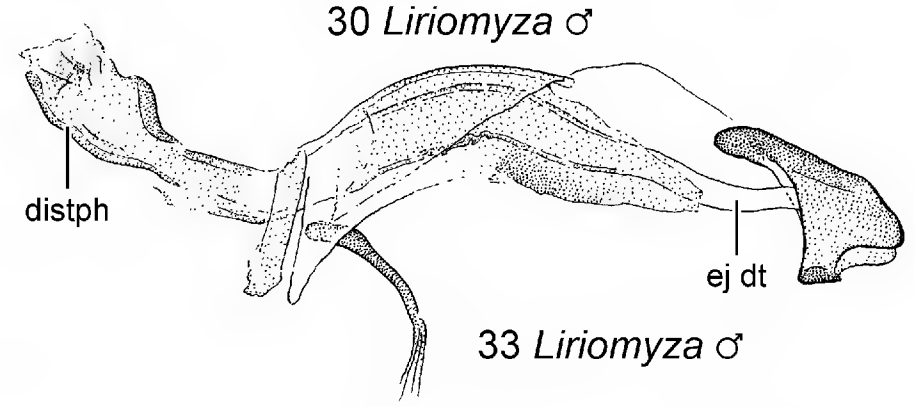
32 *Liriomyza* ♂



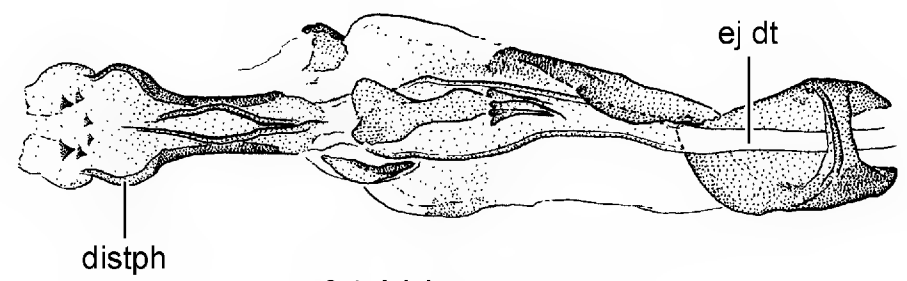
29 *Liriomyza* ♂



30 *Liriomyza* ♂



33 *Liriomyza* ♂



34 *Liriomyza* ♂

Figs 86.27–34. Male terminalia of Agromyzidae (Phytomyzinae): (27) phallus of *Liriomyza brassicae* (Riley), lateral view; (28) same, ventral view; (29) same, *L. sativae* Blanchard, lateral view; (30) same, ventral view; (31) same, *L. huidobrensis* (Blanchard), lateral view; (32) same, ventral view; (33) same, *L. trifolii* (Burgess), lateral view; (34) same, ventral view. Figs 27–34 (Lonsdale 2011, figs 59, 60, 8, 9, 126, 127, 234, 235, respectively).

Abbreviations: basph – basiphallus; distph – distiphallus; ej dt – ejaculatory duct; hypph – hypophallus; msph – mesophallus; phphs – phallophorus; pph – paraphallus.

on various crops in Central and North America, Europe, Israel, South-east Asia and Sri Lanka (Scheffer & Lewis 2001). In the Afrotropics, the species is known from the Indian Ocean islands of Madagascar, Mauritius, Réunion Is. and Seychelles and possibly Cabo Verde (CABI/EPPO 2002), although trends suggest that it has the potential to spread farther within the region. Two other similarly polyphagous and pestiferous relatives of *L. huidobrensis* in the Old World are *L. bryoniae* and *L. strigata*, which are currently restricted to Palaearctic North Africa (Dempewolf 2004).

Phytomyza is another phytomyzine genus of agricultural concern, with these primarily leaf-mining species feeding on at least 40 plant families (Winkler *et al*. 2009). There are a number of pestiferous species, with two of the most severe being *P.* (*P.*) *horticola* (Figs 19–26) (in the Afrotropical, Australasian, Oriental and Palaearctic Regions) and *P.* (*P.*) *syngenesiae* (global temperate regions, including the Canary Is.) (Winkler *et al*. 2009). These may occur in large numbers on numerous ornamental and food crops, including legumes, such as *Pisum* (Fabaceae) and many Asteraceae. A number of other global pests with more restricted diets do not occur in the Afrotropics, but the potential for damage combined with the relative ease of introduction between growing regions makes them a cause for concern: *P.* (*P.*) *carotae* (Spencer, 1966) (Europe) on carrot, *P.* (*P.*) *fuscula* Zetterstedt, 1838 (Europe and North America) and *P.* (*P.*) *nigra* Meigen, 1830 (Holarctic) on cereals, and *P.* (*P.*) *petoei* Hering, 1924 (Palaearctic, introduced into Nearctic (Boucher 2009)) on *Mentha* (Lamiaceae). Underlining the likelihood of introduction, specimens of *P.* (*P.*) *rufipes* Meigen, 1830 from South Africa, previously known only from Cabo Verde (Papp 2003), Europe and Argentina on *Brassica* (Brassicaceae), have recently been examined by the first author (van den Heever, in prep.).

In the genus *Amauromyza*, *A. flavifrons* (Meigen, 1830) can be problematic on ornamentals, such as *Dianthus* (Caryophyllaceae) and occasionally occurs on food crops, such as *Beta* and *Spinacia* (both Amaranthaceae) (Dempewolf 2004; Spencer 1973: 14), although success on *Beta* is relatively low (Scheffer 1999; Uesugi 2008). *Amauromyza flavifrons* is likely native to the Palaearctic Region, being introduced into eastern North America as late as the 1960s, where it has shown a considerable ability to thrive, extending to the Pacific by 1972, likely through human facilitated transport on host-plants. Similar transportation to the Afrotropics should be considered probable. The "Burdoc leaf-miner", *Nemorimyza maculosa* (Malloch, 1913) is another introduced pest in Africa, including the Canary Is. (Cerný *et al*. 2018) and other parts of the world (CABI/EPPO 1999).

In addition to *Liriomyza* and *Phytomyza*, cereal pests occur amongst species of the *Pseudonapomyza atra*-group, which feed exclusively on Poaceae (Zlobin 2003*a*); these species, including several Afrotropical species, can sometimes be pestiferous on young corn or rice and other cereal crops (Spencer 1973: 15). *Cerodontha* species occur on Cyperaceae, Iridaceae, Juncaceae and Poaceae (Boucher 2010) and a number of species have the potential to be pestiferous, including the African *C.* (*Poemyza*) *orbitona* (Spencer, 1960), which feeds on rice, but is normally heavily parasitised and has never been found to cause significant damage (Scheibelreiter 1973). *Cerodontha* (*C.*) *dorsalis* (Loew, 1863) occurs on 16 genera of Poaceae in the New World and Asia (Boucher 2002), including numerous food crops, and while it has never been considered pestiferous, the potential for damage in the Afrotropics is uncertain.

Phytobia differs from other Agromyzidae by feeding within the young xylem of tree trunks, twigs and roots. North temperate species are occasionally considered pestiferous in tree nurseries, where larvae leave "pith flecks" under bark (Greene 1914; Spencer 1973: 298). Species in timber of Afrotropical forests have already been reported from flecks in wood from Côte d'Ivoire in *Calpocalyx* and *Tetrapleura* (Mimosaceae), *Chidlowia* (Caesalpiniaceae), *Macaranga* and *Sapium* (Euphorbiaceae), *Trichilia* (Meliaceae), *Newbouldia* (Bignoniaceae), *Mymexylon* (Melastomataceae) and *Bertiera* (Rubiaceae), among others (Spencer 1990: 18).

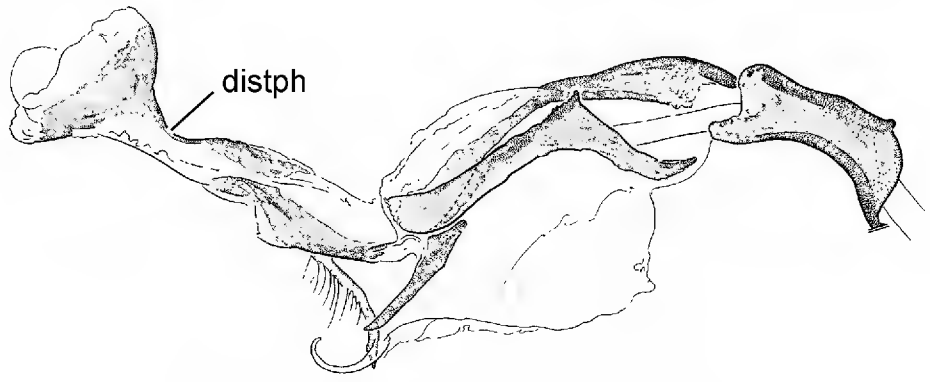
In the subfamily Agromyzinae, most problematic dicotyledon leaf-miners belong to *Tropicomyia*, with the diets of many species being highly varied. Of these, only *T. flacourthiae* (Figs 49, 50) (known to feed on at least 21 genera in 14 families) and *T. vigneae* (Séguy, 1951) (feeding on five genera of Fabaceae) currently occur in the Afrotropics (Benavent-Corai *et al*. 2005), but the potential for introduction of the remaining, mostly Old World tropical species, warrants concern. These polyphagous species include the Oriental *T. polyphaga* (Spencer, 1961) (feeding on species in at least 16 genera in 10 families), *T. atomella* (Malloch, 1914) (four genera in four families) and *T. theae* (Cotes, 1896) (six genera in five families), the Australasian *T. polyphyta* (Kleinschmidt, 1961) (27 genera in 19 families) and the Palaearctic *T. styricicola* (Sasakawa, 1954) (four genera in four families) (Benavent-Corai *et al*. 2005). Damage is often superficial, but young plants may be more severely affected, particularly those suffering from secondary fungal attack following oviposition damage. Tea and coffee are frequently attacked by these species, aside from *T. vigneae*, as well as citrus and cotton, but damage is rarely significant, likely due in no small part to high rates of parasitism (Spencer 1973: 195).

Broad polyphagy is not apparent elsewhere in the Agromyzinae, but many species deemed pestiferous are known from a range of different legumes. Most *Ophiomyia* are primarily seed- and stem-miners, but three species of extreme concern in the Afrotropics include the Afrotropical endemic *Ophiomyia centrosematis* (de Meijere, 1940) and *O. phaseoli* and *O. spencerella* (Greathead, 1969), which are widespread in Old World tropical and subtropical regions. *Ophiomyia phaseoli* is highly pestiferous on the common bean, *Phaseolus vulgaris* L., (Fabaceae), but sometimes also Soybean, Black gram, Mung bean and Pea, among others. It is considered the most important insect pest limiting bean production in sub-Saharan Africa (Ojwang *et al*. 2011), and perhaps "… the most serious of all Agromyzid pests" (Spencer 1973). Hatched larvae of *O. phaseoli* (Figs 53, 54) initially form a mine in young leaves and later enter the stem through the petiole; subsequent instars mine downwards to the tap root and return to the stem near the soil to pupariate. *Ophiomyia spencerella* is a borer in the hypocotyl and young stem tissue in mostly *Phaseolus* species, but also in *Lablab* and *Vigna* (both Fabaceae). *Ophiomyia centrosematis* is a hypocotyl- and stem-miner in *Glycine* (Fabaceae), *Phaseolus* and *Vigna*, among others. Another pestiferous species is the leaf-mining *O. pisi* (Kleinschmidt, 1961), known from *Pisum* and *Trifolium* (both Fabaceae) (Spencer 1986) and while this

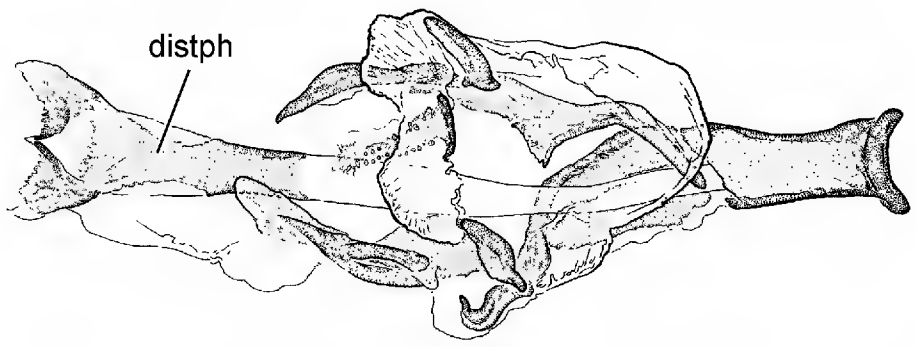
species is Australasian in distribution, the risk of introduction onto Afrotropical crops warrants mention.

Some *Melanagromyza* species also often occur in stems, including *M. sojae* (Zehntner, 1900), which attacks *Glycine* and other Fabaceae (Fig. 83). Other pestiferous Afrotropical *Melanagromyza* mine in legume seed pods, including *M. bonavistae* Greathead, 1971, *M. candidipennis* (Lamb, 1912), *M. chalcosoma* Spencer, 1959 and *M. vignalis* Spencer, 1959 (Spencer 1973: 55). *Melanagromyza obtusa* (Malloch, 1914) is also an extremely harmful pest species in the Oriental Region and while it was reared from *Cajanus cajan* (L.) (Fabaceae) in Cabo Verde in 1982 (van Harten 1988), it has not yet appeared to spread any farther in the Afrotropics; an earlier record of this species in Kenya (Khamala & Okeyo-Owour 1980) is in need of verification.

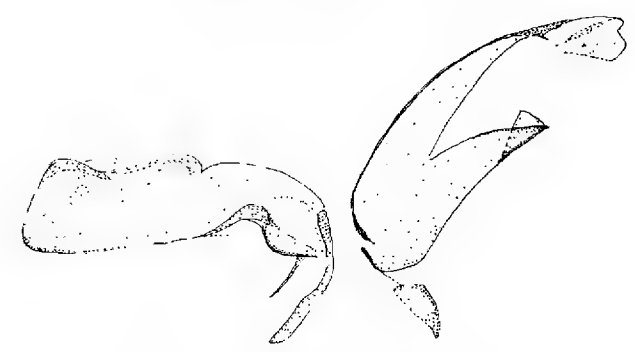
No species of the leaf-mining *Japanagromyza* are considered to be pestiferous, although potentially problematic species from the Neotropics and the southern Nearctic occur on *Glycine*, *Phaseolus* and *Vigna* (Spencer 1973: 13, 1983). Populations of *Agromyza* species infrequently reach pestiferous levels, although some north temperate Fabaceae and grass-feeding species have been known to cause problems on *Medicago*



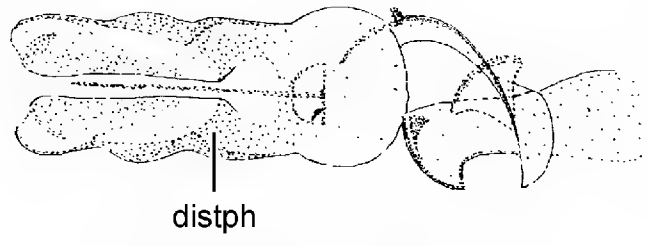
35 *Phytomyza* (*Napomyza*) ♂



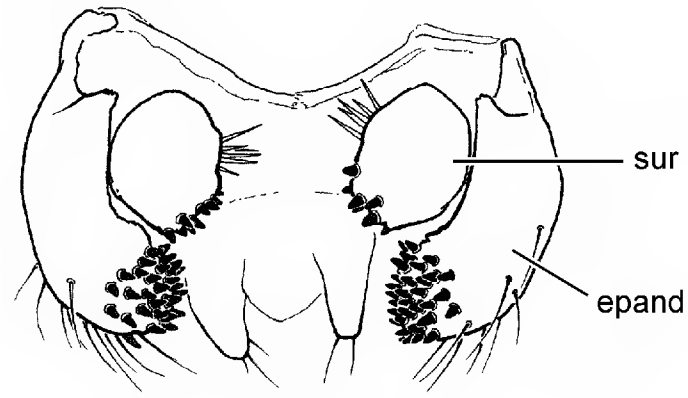
36 *Phytomyza* (*Napomyza*) ♂



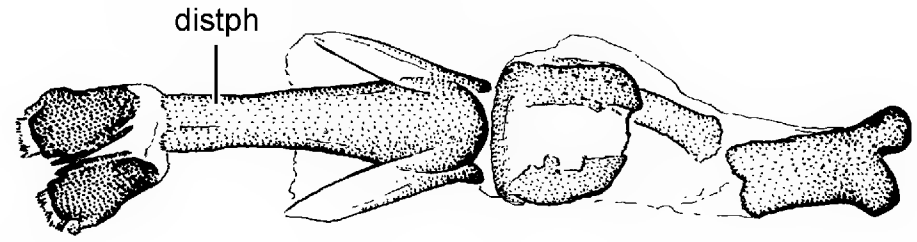
39 *Pseudoliriomyza* ♂



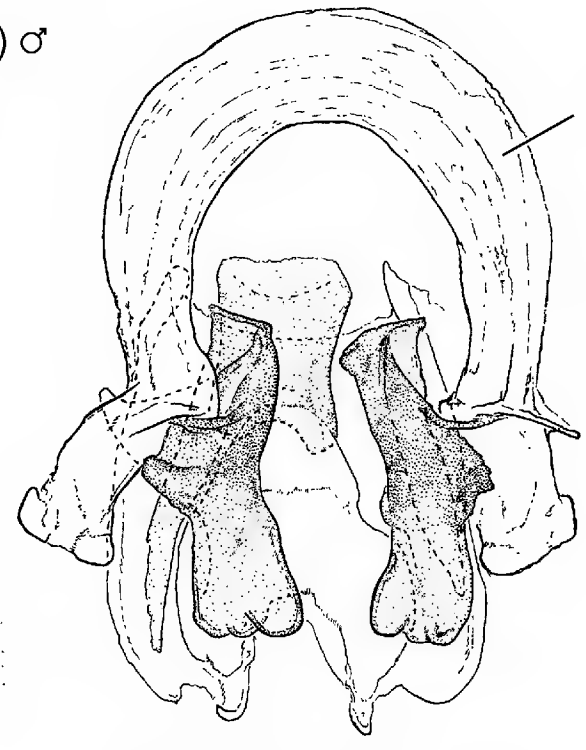
40 *Pseudoliriomyza* ♂



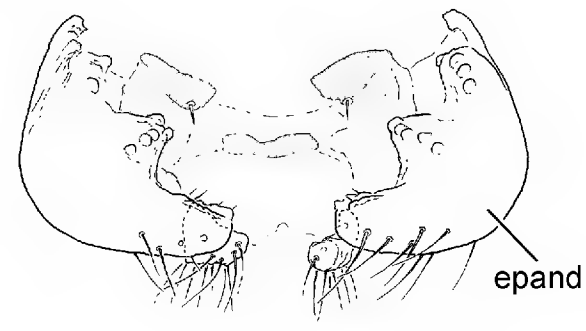
37 *Calycomyza* ♂



38 *Calycomyza* ♂



41 *Pseudoliriomyza* ♂



42 *Pseudoliriomyza* ♂

Figs 86.35–42. Male terminalia of Agromyzidae (Phytomyzinae): (35) phallus of *Phytomyza* (*Napomyza*) sp., lateral view; (36) same, ventral view; (37) external terminalia of *Calycomyza humeralis* (von Roser), ventral view; (38) same, phallus, ventral view; (39) phallus of *Pseudoliriomyza cordiae* (Spencer), lateral view; (40) same, ventral view; (41) same, internal terminalia (excluding phallus), ventral view; (42) same, external terminalia, ventral view. Figs 39, 40 (Spencer 1966, figs 22, 23).

Abbreviations: distph – distiphallus; epand – epandrium; hypd – hypandrium; sur – surstylus.

(Fabaceae) and cereal crops (Spencer 1973: 13). One South African species, *A. ocularis* Spencer, 1961, can attain high populations in wheat fields (Adendorff 2010).

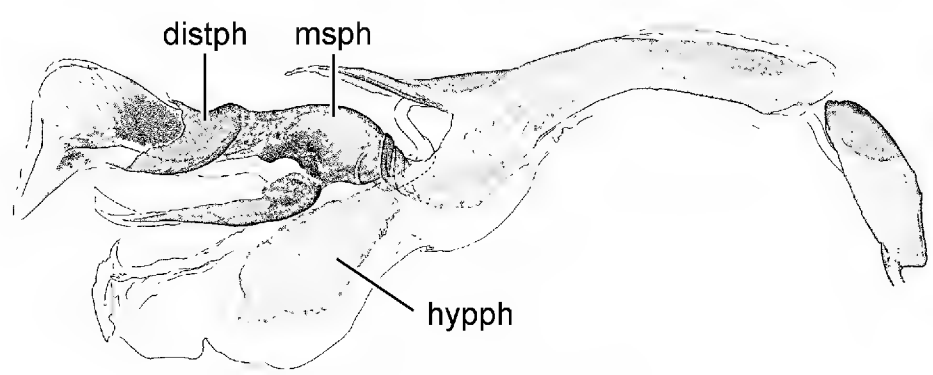
Recently, some species have been introduced to the Afrotropics from other zoogeographical regions as agents against weeds and one tree, including *Calycomyza eupatorivora* Spencer, 1973, from the Neotropics against *Chromolaena* (Asteraceae); *Calycomyza solidaginis* (Kaltenbach, 1869), from the Palaearctic and an undescribed species of *Pseudonapomyza* from Argentina against *Tecoma* (Bignoniaceae) (Madire *et al*. 2011*a*) (Fig. 85). Attempts to control *Lantana* (Verbenaceae) have utilised *Ophiomyia lantanae* (Froggatt, 1919) from Australia and *O. camarae* Spencer, 1963 and *Calycomyza lantanae* (Frick, 1956) from the New World; *C. lantanae* has been introduced throughout much of the Old World for this purpose, with releases in Australia, China, Guam Is., Hawaii, India, Malaysia, Micronesia and Saudi Arabia; in the Afrotropics, it was introduced into Ethiopia and Madagascar (Urban *et al*. 2010*a*, *b*), Mozambique (Süss *et al*. 2008) and South Africa (Cilliers 1983), to name but a few.

Classification

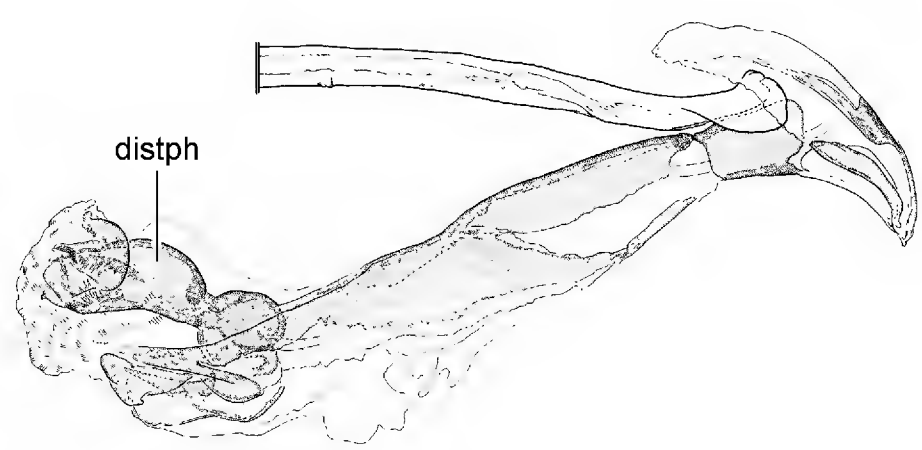
The family Agromyzidae has historically been treated as a representative of the superfamily Opomyzoidea, often following the classification presented by McAlpine (1989: 1454). This higher phylogenetic framework was not supported by Griffiths (1972: 213), who placed the Agromyzidae in his prefamily Agromyzoinea, that only otherwise included the "opomyzoid" family Clusiidae. Close examination of the Clusiidae, however, has revealed no affinities with the Agromyzidae, aside from the presence of putatively ancestral wing and chaetotaxy characters. Within the Opomyzoidea, similarities in life history and morphology have also allied the Agromyzidae to the Fergusoninidae (McAlpine 1989: 1458), an Australasian family with characteristic larvae that feed in galls formed by symbiotic nematodes. Any morphological similarities with the Fergusoninidae, however, are almost certainly a result of convergence, due to larval feeding on living plant tissue (O. Lonsdale, unpubl.). With strong support for a polyphyletic Opomyzoidea (Winkler *et al*. 2010), superfamily relationships of the Agromyzidae are currently uncertain.

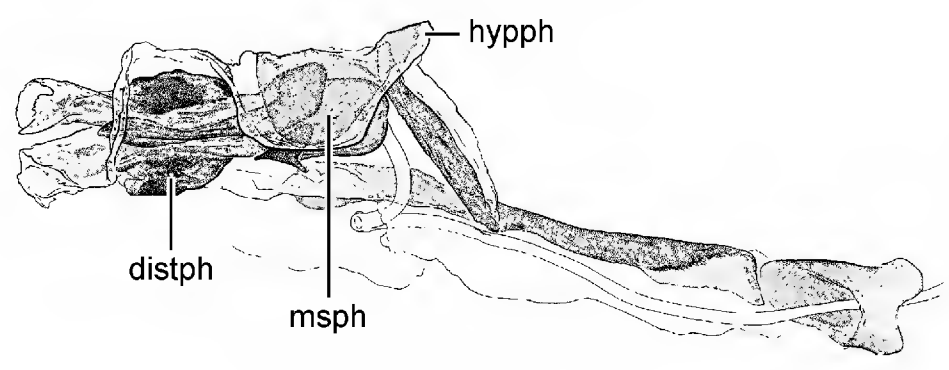
Most authors divided the Agromyzidae into two subfamilies, Agromyzinae and Phytomyzinae, following the original system devised by Fallén (1823*a*: 1, *b*: 1). An alternate classification proposed by Spencer (1990: 388) treated the Agromyzinae as the *Penetagromyza*-group and the Phytomyzinae as the *Napomyza*-, *Phytobia*- and *Phytoliriomyza*-groups. This system was not widely accepted and is partially incongruent with the morphological and molecular results of Dempewolf (2001, 2005: 423) and Scheffer *et al*. (2007), which support the original two subfamily system.

Hypotheses on finer genus-level relationships have been turbulent, with many concepts depending largely on preconceived ancestral states, regarding feeding behaviour, host usage and body size. These have been largely overturned by recent quantitative phylogenetic reconstructions, as summarised in Scheffer *et al*. (2007), which mostly support small body size and leaf-mining habits as ancestral. Reworking of these phylogenetic relationships to produce genus groupings that are both monophyletic and practical for the purposes of identification and communication are ongoing, including those already presented by Lonsdale (2014), Winkler *et al*. (2009) and Zlobin (1994, 1997, 1999, 2003*a*).

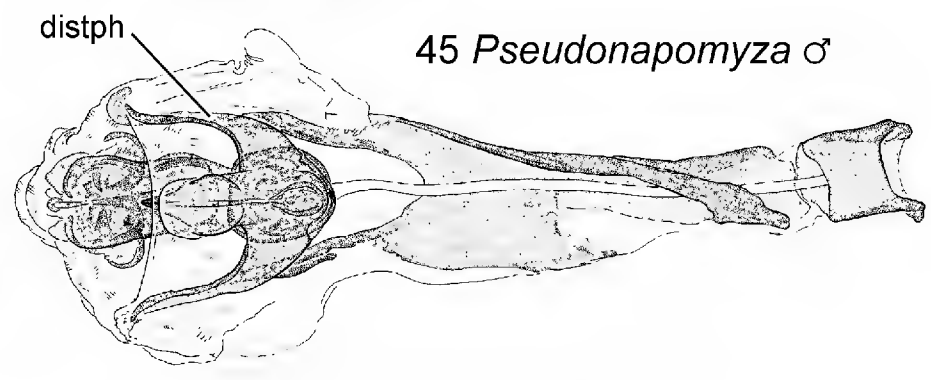


43 *Phytobia* ♂





44 *Phytobia* ♂



45 *Pseudonapomyza* ♂

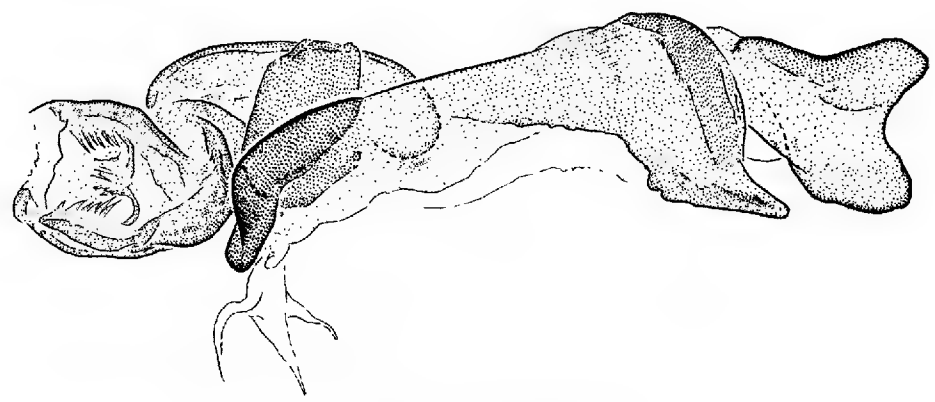
46 *Pseudonapomyza* ♂

Figs 86.43–46. Male terminalia of Agromyzidae (Phytomyzinae): (43) phallus of *Phytobia* sp., lateral view; (44) same, ventral view; (45) same, *Pseudonapomyza* sp., lateral view; (46) same, ventral view.

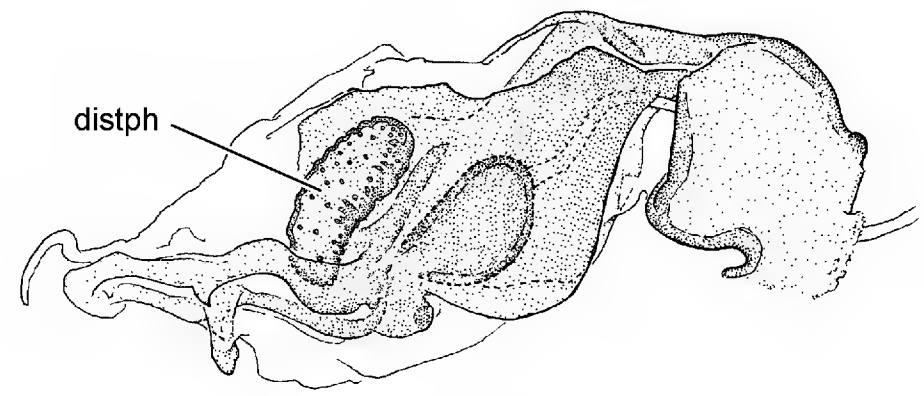
Abbreviations: distph – distiphallus; hypph – hypophallus; msph – mesophallus.

Within the Agromyzinae, there is strong support for monophyly of *Agromyza* and for monophyly of the "*Ophiomyia* genus-group" (Dempewolf 2001; Lonsdale 2014). *Japanagromyza* shares characteristics of both groups and has historically been treated as an "intermediate" between the two clades, although additional study is required to resolve the relationships and internal branching of this diverse genus (Lonsdale 2013). Phylogenetic reconstruction of lineages within the *Ophiomyia* genus-group is also required to resolve a number of outstanding problems, as discussed by Lonsdale (2014), who provided some initial steps by synonymising several small, spurious genera and clarifying some natural units useful as genera. Resolving phylogenetic relationships within *Ophiomyia* is now of particular importance to better define the genus or discover whether its component lineages better lend themselves to splitting.

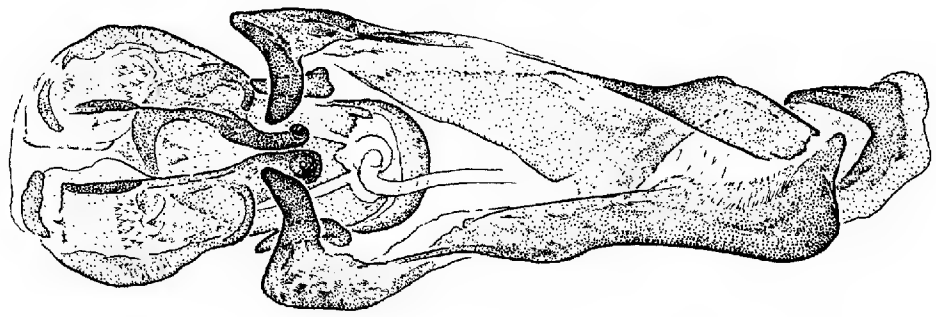
Within the Phytomyzinae, one group of genera consisting of *Calycomyza*, *Galiomyza* Spencer, *Haplopeodes* Steyskal,



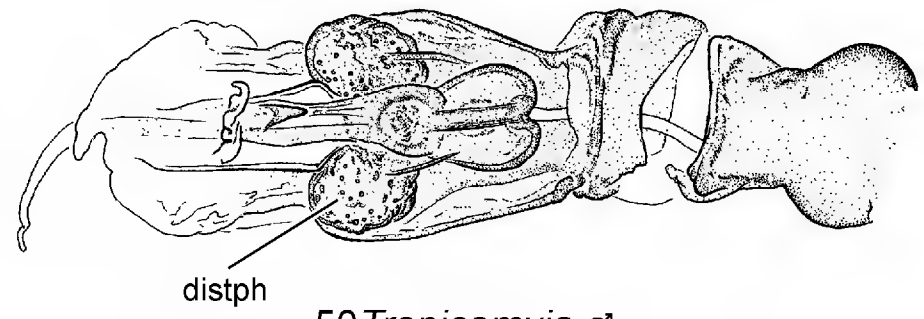
47 *Agromyza* ♂



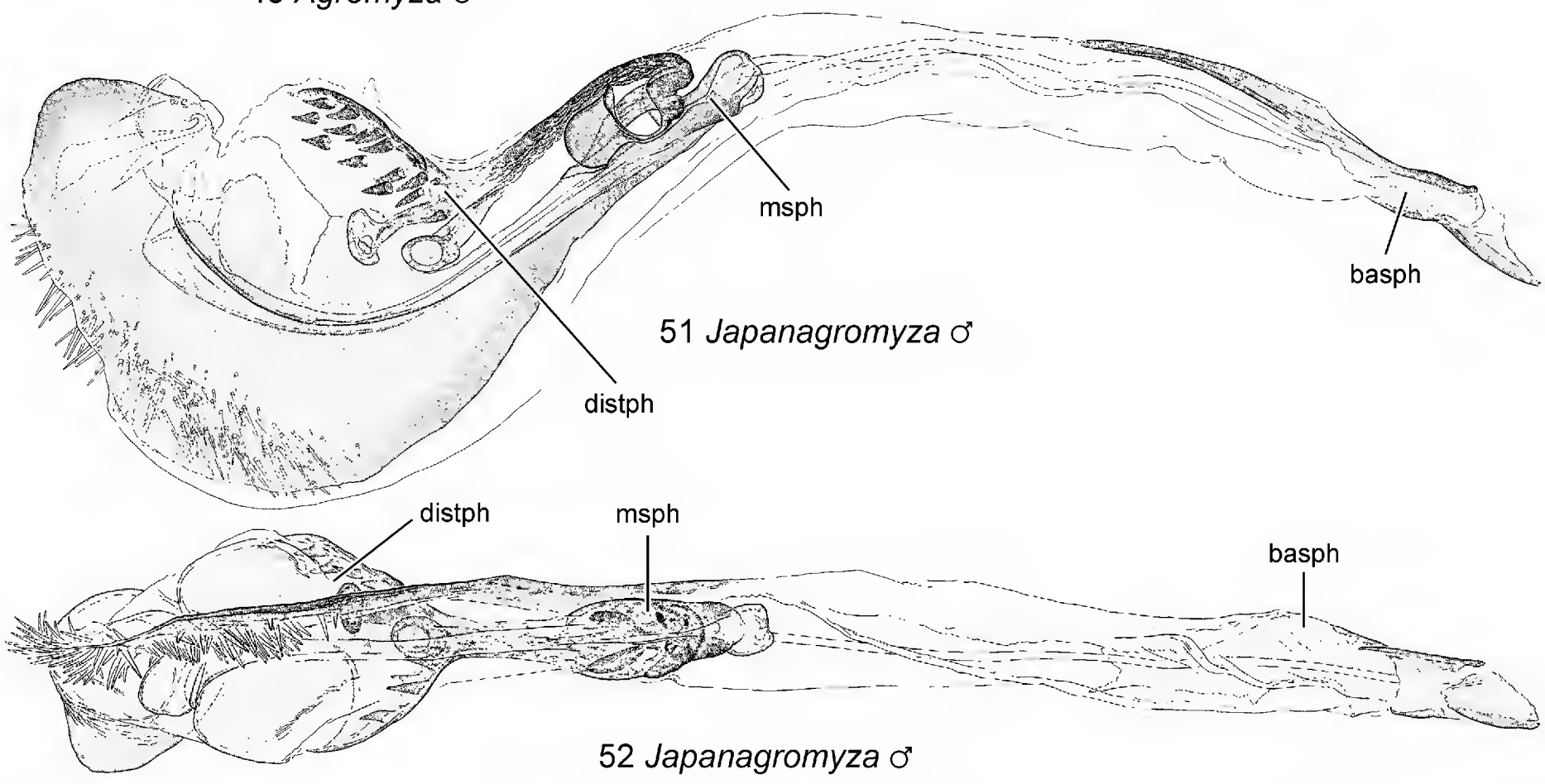
49 *Tropicomyia* ♂



48 *Agromyza* ♂



50 *Tropicomyia* ♂



51 *Japanagromyza* ♂

52 *Japanagromyza* ♂

Figs 86.47–52. Male terminalia (phallus) of Agromyzidae (Agromyzinae): (47) *Agromyza* sp., lateral view; (48) same, ventral view; (49) *Tropicomyia flacourthiae* (Séguy), lateral view; (50) same, ventral view; (51) *Japanagromyza dolobrata* Lonsdale, lateral view; (52) same, ventral view. Figs 49, 50 (Lonsdale 2014, figs 94, 93, respectively), Figs 51, 52 (Lonsdale 2013, figs 13, 14).

Abbreviations: basph – basiphallus; distph – distiphallus; msph – mesophallus.

Liriomyza, *Metopomyza* Enderlein and *Phytoliriomyza* Hendel, is characterised by tubercle-like setae on the posterodistal margin of the epandrium and surstylus (as in Fig. 37). Excluding *Calycomyza*, species are sometimes difficult to place to genus without dissection of the male terminalia and generic boundaries are ill-defined and frequently overlap, necessitating additional phylogenetic study.

The "*Napomyza* group" of Spencer has been relatively stable, although *Aulagromyza* Enderlein (which likely consists of at least two non-related lineages) and *Gymnophytomyza* Hendel, are now also well-supported as relatives (Dempewolf 2001; Scheffer *et al*. 2007). Extension of the costal vein to vein R_{4+5} (not vein M_1) and costalisation of the wing veins characterise most species (Figs 17, 18). *Phytomyza* is the most morphologically diverse taxon in the group, which has caused considerable confusion at the genus-level with regards to classification. Many of these difficulties were resolved by Winkler *et al*. (2009), although much still remains to be resolved amongst the early branching taxa of the group. The classification proposed in that study is followed here, as the *Phytomyza sensu lato* outlined in that paper allows for a single entity of likely monophyly that is diagnosed by easily recognisable, external morphological characters, *i*.e., fronto-orbital setulae proclinate; costal vein only extending to vein R_{4+5}; M_1 weak/spectral; and crossvein *dm–m* absent or situated basally. Within *Phytomyza sensu lato*, *Napomyza* and *Ptochomyza* Hering, are supported as monophyletic and still recognised, but they are treated as subgenera, as they each render *Phytomyza sensu lato* paraphyletic; *Chromatomyia* Hardy is no longer recognised, as Winkler *et al*. (2009) discovered the genus to be polyphyletic, with the type species deeply embedded in *Phytomyza sensu stricto*, easily justifying synonymy. Previous definitions of the genus, still applied by some workers, who are yet to provide quantitative support for retention of the prior system, recognise an artificial entity requiring examination of select terminalia or immature characters for diagnosis. This approach is not recommended, however, as it is impractical for diagnosis, immature characters are problematic for use in agromyzid classification (Dempewolf 2005: 407; Lonsdale 2014) and monophyly should be considered an essential criterion for higher-level groupings. The second author expresses doubts regarding recent classification changes to *Ophiomyia* and *Phytomyza* outlined above.

Winkler *et al*. (2010) summarised the knowledge of fossil mines of Agromyzidae. Larval feeding tracks in fossil wood are by far the most abundant signs of the presence of Tertiary Agromyzidae, but to date no fossil adult fly has been confirmed by a specialist (Tschirnhaus & Hoffeins 2009).

Identification

Identification tools and descriptions for Afrotropical taxa are primarily found in a series of papers published by Spencer from 1959–1965 (Spencer 1959, 1960*a*, *b*, 1961*a*, *b*, *c*, 1963*a*, *b*, 1964, 1965). The first of these include complete species identification keys and some of the later works provide amendments with the description of new species. Additional species descriptions for various genera are also published in: Černý (2011), Černý & Zlobin (2008), Deeming (2006), Greathead (1969, 1971), Lonsdale (2013), Spencer (1973, 1985, 1991) and Zlobin (1993*a*, *b*).

The Afrotropical fauna is considered relatively depauperate in species (Cogan 1980: 639), but this is likely an artefact of limited sampling and study. A number of collections, including that of the writers, are indicative of this diversity, encompassing large numbers of specimens and undescribed species, mostly belonging to *Melanagromyza* and *Ophiomyia*; undescribed *Pseudonapomyza* are also particularly abundant, especially in equatorial countries. Much remains to be discovered of the regional fauna, including not just new species, but also new locality records and host data. Most genera of Agromyzidae are in need of revision in the Afrotropics and an identification key is only available for the genus *Japanagromyza* (Lonsdale 2013).

At least 553 publications deal with Afrotropical Agromyzidae. Three hundred and twenty-four valid Afrotropical species are listed by Černý & Tschirnhaus (2014); one additional species was added by Lonsdale (2015) (World 3,127 as of July 2019). Most species were recorded from South Africa (130), Kenya (83), Madagascar (56) and Ethiopia (48). Agromyzidae are best micro-pinned in the field for later double-mounting (see Chapter 2).

Key to genera of Afrotropical Agromyzidae

1. Subcostal wing vein (*Sc*) well-developed along entire length, fused to vein R_1 before reaching costal vein (*C*) (e.g., Figs 11, 12); vein R_1 sinuous for short distance just before reaching costal vein (*C*), sometimes thickened, relatively straight in some *Agromyza*, which have abdomen with distinct stridulatory file on lateral margin of syntergite 1 + 2 (e.g., Fig. 5); vein R_{4+5} often ending as close, or closer to wing apex, compared to vein M_1; head with lunule often with medial furrow, well-sclerotised, flat to bulging (e.g., Figs 6, 7) (recessed in some *Agromyza* and poorly preserved material) (AGROMYZINAE) 2

– Subcostal wing vein (*Sc*) either ending freely in cell or continuing to costal vein (*C*) as a fold, or atrophied vein (e.g., Figs 13–18); vein R_1 straight, not deviating before reaching costal vein (C), rarely thickened apically (some *Phytobia*); vein M_1 usually closer to wing apex, as compared to vein R_{4+5} (except *Phytobia*) (e.g., Fig. 13); abdomen with lateral margin of syntergite 1 + 2 never with stridulatory file; head with lunule without medial furrow (except some *Phytobia*), often soft, usually flat or recessed (e.g., Figs 9, 10) (PHYTOMYZINAE). 9

2. Thorax with prescutellar acrostichal seta; halter white, at least apically (black in some *Agromyza*, partially black in some *Japanagromyza*) 3

– Thorax without prescutellar acrostichal seta; halter black (white in *Ophiomyia abnormalis* (Malloch, 1913)) 5

3. Abdomen with lateral margin of syntergite 1 + 2 with dark, strongly sclerotised stridulatory file (Fig. 5) . . . . . *Agromyza* Fallén

– Abdomen with lateral margin of syntergite 1 + 2 weakly sclerotised, sometimes rounded, or irregular in outline, but without stridulatory file 4

4. Thorax usually with 2 well-developed dorsocentral setae, sometimes 3; head with ocellar triangle usually large, well-developed; fronto-orbital setulae present; fore tibia usually with medial seta posterolaterally; halter usually brown in part; body sometimes with metallic sheen . . . . . *Japanagromyza* Sasakawa [in part]

– Thorax with 4 dorsocentral setae (3 postsutural, 1 presutural); head without ocellar triangle and fronto-orbital setulae; fore tibia bare; halter white; body non-metallic . . . . . Undescribed genus

5. Head with clypeus with anterior margin truncated, anterolateral corners distinct (Fig. 8); clypeus sometimes parallel-sided; gena often anteriorly produced, if so then males sometimes with multiplicated vibrissae forming upcurved "fasciculus" or "horn" (Fig. 8); face often carinate, usually with medial bulb or swelling between antennal bases (Fig. 8); fore tibia without posteromedial seta, mid tibia with 0–1 posteromedial seta; abdomen uncommonly with slight metallic sheen . . . . . *Ophiomyia* Braschnikov

– Head with clypeus U-shaped, rounded anteromedially, but if slightly truncated along anterior margin (some *Melanagromyza*), then with one or more of the following three characters: eye setulose dorsally (e.g., Fig. 6), fore tibia with posteromedial seta, mid tibia with > 1 posteromedial setae; head with gena uncommonly produced slightly (some *Melanagromyza*), never pointed; vibrissa single, not multiplicated; face rarely with shallow carina; entire thorax and abdomen strongly metallic 6

6. Fore tibia with small to well-developed seta medially on posterolateral surface; costal wing vein (C) invariably extending to vein M_1 (e.g., Fig. 12) 7

– Fore tibia without posterolateral setae medially; costal wing vein (C) extending to vein M_1 or vein R_{4+5} 8

7. Head with ocellar triangle barely reaching beyond level of posterior fronto-orbital seta; frons and lunule smooth, with faint pruinosity; orbital plate along eye narrow, not raised or conspicuous, level with remainder of frons; compound eye bare, or with few small, inconspicuous setulae; hind tibia with cleaning comb (formed of row of similar adjoining erect setulae) on inner end; male terminalia with epandrium usually flat on posteroventral margin, sometimes extended into long lobate process (but not as below); basiphallus asymmetrical (Figs 51, 52); often with left and right sides divided; mesophallus basal to distiphallus, arranged linearly; distiphallus often forked or membranous, usually elongate and flagellate; without paired ventrobasal tubules. . . . . *Japanagromyza* Sasakawa [in part]

– Head with ocellar triangle exceeding level of posterior fronto-orbital seta, sometimes reaching lunule; frons with texture variable, lunule smooth; orbital plate distinct, often raised or bulging; compound eye often conspicuously setulose in upper ⅓, especially in males (Fig. 6); hind tibia without cleaning comb; male terminalia with epandrium usually produced into small triangular point on posteroventral margin; basiphallus symmetrical, ring- or U-shaped (Figs 55, 56); mesophallus usually inserted ventromedially into distiphallus; distiphallus variable, but usually with stout, globose base; with paired ventrobasal tubules flanking mesophallus . . . . . *Melanagromyza* Hendel [in part]

8. Thorax (and often head and abdomen) usually with green, blue or coppery metallic sheen; compound eye often conspicuously setulose dorsally, particularly in males (Fig. 6); mid tibia with 1–3 medial setae posterolaterally; male terminalia with basiphallus symmetrical, ring- or U-shaped (Figs 55, 56); distiphallus with paired ventrobasal tubules flanking mesophallus. . . . . *Melanagromyza* Hendel [in part]

– Thorax without metallic sheen; compound eye bare; mid tibia with 0–1 medial setae posterolaterally; male terminalia with base asymmetrical (Figs 49, 50); distiphallus without paired basal tubules . . . . . *Tropicomyia* Spencer

9. Head with lunule relatively high, at least as high as antennal pedicel (compare Figs 9 and 10), often convex, conspicuously produced into emarginate frons, shallow and semicircular to long and narrow; wing crossvein *dm–m* invariably present in Afrotropical species; scutellum with anterolateral seta sometimes reduced or absent; male terminalia with long narrow lobe produced from venter of subepandrial sclerite, often with terminal claw; distiphallus almost invariably long, bifid, with apex often swollen or slightly separated, sometimes forming small bell-like funnel . . . . . *Cerodontha* Rondani 10

– Head with lunule shallow, usually flat, if as high as antennal pedicel (some *Phytomyza*; Fig. 9), then fronto-orbital setulae proclinate, wing crossvein *dm–m* absent (Figs 16–18), or virtually level with crossvein *bm–m*; scutellum with anterolateral seta well-developed; male terminalia rarely with one pair of long

processes developed from subepandrial sclerite as above (some *Liriomyza*); distiphallus various (e.g., Figs 27–36, 38, 40, 46), sometimes long and bifid, but almost never with apex separated into small funnel (some *Phytomyza*) 15

10. Antennal postpedicel pointed anterodorsally (Fig. 10); scutellum with only single pair of marginal setae at apex . . . . . *Cerodontha sensu stricto*

– Antennal postpedicel rounded; scutellum with 2 pairs of marginal setae (*Poemyza* rarely with 1 pair) 11

11. Thorax with elongate prescutellar acrostichal seta; head with lunule slightly higher than wide, gradually tapering to a point dorsally, well-sclerotised, light brown to brown, clothed in short velvety pubescence . . . . . *Cerodontha* (*Butomomyza* Nowakowski)

– Thorax without elongate prescutellar acrostichal seta (present in some non-Afrotropical species); if head with lunule higher than wide, then not as above 12

12. Head with lunule narrow, higher than wide, sometimes sunken beneath prominent orbital plates; often shiny with surface minutely textured, sometimes with minute black scales or spiculae . . . . . *Cerodontha* (*Poemyza* Hendel)

– Head with lunule as wide or wider than high, surface smooth with variable pubescence 13

13. Male terminalia with distiphallus straight or bent, extremely short, sometimes with 2 short dark tips, indistinguishable as paired tubules; colour yellowish grey; femora yellow, except base; abdominal tergites with slight metallic sheen . . . . . *Cerodontha* (*Icteromyza* Hendel) [in part]

– Male terminalia with distiphallus with single pair of long, well-sclerotised tubules; colour otherwise. 14

14. Head with lunule well sclerotised, meeting anterior margin of frons, partly flat above; head usually grey to dark brown; antennae widely separated; male postpedicel sometimes enlarged and/or axe-shaped, sometimes also with long, conspicuous setulae . . . . . *Cerodontha* (*Dizygomyza* Hendel)

– Head with lunule bulging, soft, usually expanded above sunken anterior margin of frons; head with lunule and sometimes frons bright yellow; antennae approximated; male postpedicel not larger than those of females, with setulae moderately sized . . . . . *Cerodontha* (*Icteromyza* Hendel) [in part]

15. Wing vein R_{4+5} as close or closer to wing tip than vein M_1 (Fig. 13); membrane sometimes patterned; head with lunule usually silvery or with shiny pubescence; frons sometimes with proclinate setulae directly above lunule; relatively stout-bodied, often large (wing length usually: 2.5–5.6 mm) . . . . . *Phytobia* Lioy

– Wing vein M_1 closer to wing tip than vein R_{4+5} (e.g., Figs 14–18); membrane never patterned; head with lunule not as above; usually slender-bodied, small (wing length usually: < 2.5 mm). 16

16. Costal wing vein (C) ending at or slightly beyond vein R_{4+5} (e.g., Figs 15–18); male terminalia with epandrium and surstylus usually without tubercle-like setae (e.g., Figs 19–21) 17

– Costal wing vein (C) extending to vein M_1 (e.g., Fig. 14); male terminalia with epandrium and surstylus usually with at least one tubercle-like seta each 20

17. Head with fronto-orbital setulae reclinate, upright or absent; antennal postpedicel often with narrow dorsoapical point; halter sometimes black in part; fore tibia sometimes with posterolateral seta; mid tibia often with 1–4 posterolateral setae; body colour usually mostly black, sometimes ochreous . . . . . *Pseudonapomyza* Hendel

– Head with fronto-orbital setulae proclinate (Fig. 9); antennal postpedicel various, usually ovate, very rarely with shallow dorsoapical point; halter whitish, uncommonly slightly brownish; fore and mid tibia without posterolateral seta/e; body colour various, dark or yellowish. . . *Phytomyza* Fallén *sensu lato* 18

18. Radial wing veins ending relatively close to wing apex, *i*.e., costal section between veins R_{2+3} and R_{4+5} < 2.0 × length of costal vein (C) between veins R_{4+5} and M_1 (Fig. 17); discal medial crossvein (*dm–m*) distinctly distal to radial–medial crossvein (*r–m*), if present . . . . . *Phytomyza sensu stricto*

– Radial wing veins inserted nearer to base of wing on costal vein (C), *i*.e., costal section between veins R_{2+3} and R_{4+5} at least 2.5 × length of costal vein (C) between veins R_{4+5} and M_1 (Fig. 18); discal medial crossvein (*dm–m*) virtually in line with radial–medial crossvein (*r–m*), if present 19

19. Wing with discal medial crossvein (*dm–m*); relatively large-bodied (wing length usually: > 2.0 mm); thorax with scutum mostly dark with grey pruinosity; 4 well-developed dorsocentral setae present; male terminalia with distiphallus formed of long membranous tubule, with apical ring and either dorsal or ventral sclerotised strip (Figs 35, 36) . . . . . *Phytomyza* (*Napomyza* Westwood)

– Wing without discal medial crossvein (*dm–m*) (Fig. 18); most species relatively small-bodied (wing length: 1.0–1.4 mm), sometimes larger (1.8–2.3 mm); thorax with scutum yellow with brownish fasciae;

only posterior 2 dorsocentral setae distinctly larger than surrounding setulae, with third sometimes slightly larger; male terminalia with distiphallus with sclerotised base and membranous bifid apex . . . . . *Phytomyza* (*Ptochomyza* Hering)

20. Thorax usually with 2 strong dorsocentral setae, with third and fourth pairs very short or barely longer than surrounding setulae; head and notopleuron pale yellow, with antenna and most of remaining notum black; male terminalia with epandrium and surstylus each with dense cluster of tubercles (Fig. 37) . . . . . *Calycomyza* Hendel

– Thorax with 3 or more pronounced dorsocentral setae, if only 2 present, then colouration never as above; male terminalia with tubercles on surstylus and epandrium often reduced, but if present in large numbers, then almost invariably arranged in rows 21

21. Halter entirely black and/or male terminalia with distiphallus compact, black, surrounded by minutely spinulose membrane; head with gena usually ⅓–½ height of compound eye; male terminalia with sclerotisation on sperm pump large and bowl-shaped . . . . . *Amauromyza* Hendel

– Halter white, apical surface sometimes brown, male terminalia with distiphallus without spinulose membrane; head with gena usually < ⅓ eye height, but sometimes as above; male terminalia with sclerotisation on sperm pump sometimes bowl-shaped (usually not enlarged), but more commonly reduced or band-like 22

22. Head with fronto-orbital setulae proclinate to reclinate; compound eye minutely setulose; frons with margins silvery pubescent; scutellum entirely brown or with ill-defined yellowish medial fascia; halter with apical surface light brown. . . . . *Phytoliriomyza* Hendel [in part]

– Head with fronto-orbital setulae upright to reclinate, sometimes absent, but never proclinate; compound eye bare or with few scattered microtrichia; frons with margins rarely reflective as above; scutellum sometimes brown or yellowish medially, but usually with strong, clearly defined medial yellow fascia; halter entirely white 23

23. Thorax with only posterior 3 dorsocentral setae well-developed, fourth not larger than surrounding setulae; without postsutural intra-alar seta; male terminalia with each side of epandrium with raised protuberances in 2 rows (Fig. 42); hypandrium thick and semicircular (Fig. 41) . . . . . *Pseudoliriomyza* Spencer

– Thorax with anterior (fourth) dorsocentral setae well-developed; with postsutural intra-alar seta; male terminalia with epandrium without rows of protuberances; hypandrium thin and more narrowly arched 24

24. Head with broad, sclerotised ocellar triangle, orbital plates joined to form acute angle, altogether resembling the letter "M"; orbital plate brown, well-delimeted and well-sclerotised (contrasting weakly sclerotised frons, also usually brown); male terminalia with surstylus with 1 and epandrium with 2 rows of tubercle-like setae . . . . . *Metopomyza* Enderlein

– Head with ocellar triangle and orbital plate usually separate, but if joined along posterior margin of frons, then broadly joined by intervening space (connecting angle broadly rounded or squared); if orbital plate and frons brown (as above), then both weakly sclerotised; male terminalia rarely as above (some *Phytoliriomyza*), usually with 0–1 tubercle-like setae, or with more numerous scattered tubercles 25

25. Head with 1 or more of the following: frons with light reflective pruinosity anterolaterally, or entirely clothed in tiny greyish scales; antennal postpedicel slightly elongate, entirely black; large portions of scutum and scutellum matt grey or tan-coloured; male terminalia with epandrium and surstylus often with rows of large, dark tubercle-like setae. . . . . *Phytoliriomyza* Hendel [in part]

– Head with frons never with reflective pruinosity; antennal postpedicel yellow to dark brown; thorax with scutum and scutellum usually subshiny to shiny, sometimes pruinose or matt grey, but never with tan-coloured pruinescence; male terminalia with epandrium and surstylus usually with 1 or 2 tubercle-like setae 26

26. Wing without discal medial crossvein (*dm–m*); thorax with grey pruinosity; male stridulatory organ invariably absent; male terminalia with phallus small, membranous, with sclerotised base; ejaculatory duct with apical section clear, of equal width throughout its length; surstylus in contact with subepandrial sclerite . . . . . *Haplopeodes* Steyskal

– Wing with discal medial crossvein (*dm–m*) (Figs 2, 3) (absent in some non-Afrotropical species); thorax sometimes with grey pruinosity, often bare to sparsely pruinose; male often with raised stridulatory organ on abdominal membrane anterolaterally (Figs 3, 4); male terminalia with phallus with at least 2 distinct sclerotised segments (Figs 27–34); ejaculatory duct with apical section abruptly dilated and pigmented; surstylus separated from subepandrial sclerite . . . . . *Liriomyza* Mik

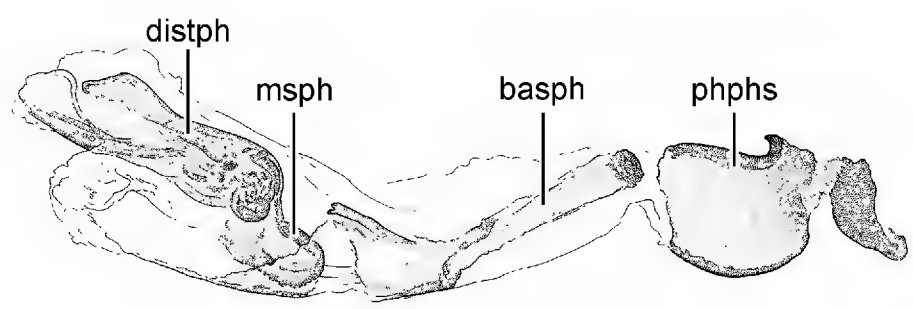
Synopsis of the fauna

The family Agromyzidae comprises 3,127 valid species globally, 325 of which occur in the Afrotropical Region. The subfamily Agromyzinae comprises 1,034 valid species globally, 191 of which occur the Afrotropics; the subfamily Phytomyzinae 2,093 valid species globally, 134 Afrotropical.

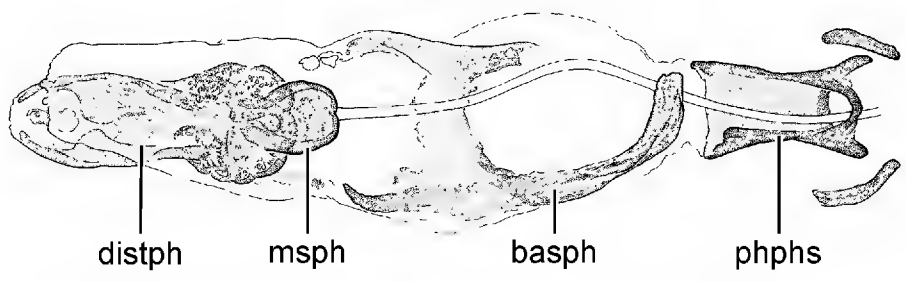
***Agromyza* Fallén** (Agromyzinae)**.** A genus of 203 valid species occurring in all zoogeographical regions, except Antarctica. Twenty-three species are recorded from the continental Afrotropics, the Arabian Peninsula, Cabo Verde and Madagascar. Both sexes of *Agromyza* have a dark, well-sclerotised stidulatory file along the lateral margin of the fused abdominal tergites 1 and 2 (Fig. 5) (reduced in one undescribed species from the Canary Is. and Jordan) and a well-developed pair of prescutellar acrostichal setae (also in many *Japanagromyza*). Species usually also have at least three or four well-developed dorsocentral setae, but in many cases only the posterior two are immediately obvious, with the anterior setae absent or slightly larger than the surrounding setulae. Most species are leaf-miners, including those belonging to a particularly speciose lineage with a characteristic phallus (Figs 47, 48), specialising on grasses; a minority feed in stems, two of which induce galls. While the genus is thought to be most diverse in the north temperate regions, numerous species remain undescribed globally.

***Amauromyza* Hendel** (Phytomyzinae)**.** A genus of 60 valid species occurring in all zoogeographical regions, except Antarctica, with most taxa known from the Nearctic and Palaearctic Regions. A single species, *A. triseta* (Spencer, 1959), is recorded from South Africa (Spencer 1959), although an undescribed species is also known from near Kabarole in Uganda (M. von Tschirnhaus, unpubl.). External morphological features are particularly diverse across the genus, often necessitating examination of the male terminalia for confident generic placement. *Amauromyza* is currently defined on the basis of a bowl-shaped sclerite on the sperm pump and a broadly rounded hypandrium. Both of these terminalia features occur throughout the subfamily, however, sometimes in tandem, as in the monotypic *Pseudoliriomyza* Spencer. A dark spinulose membrane surrounds the distiphallus of many species, including the extralimital *A. flavifrons* (Meigen, 1830), which is sometimes more useful for diagnosis. Larvae are known to be stem-borers and leaf-miners in dicotyledons, with only *A. belamcandae* Sasakawa, 1981, from Japan developing in the monocotyledon *Belamcanda* (Iridaceae).

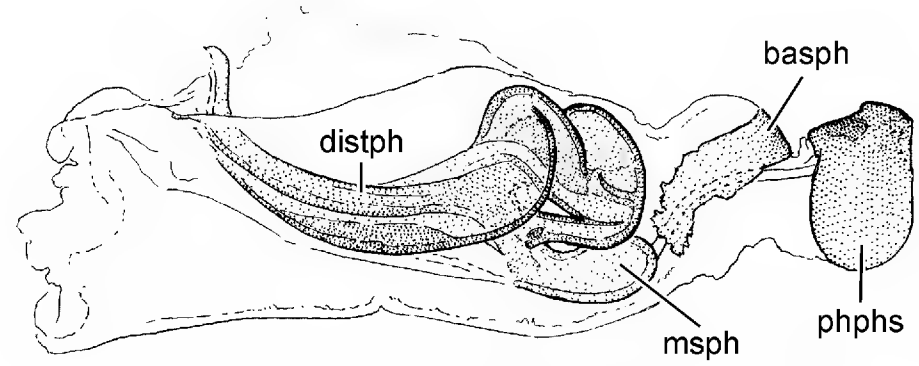
***Calycomyza* Hendel** (Phytomyzinae)**.** A genus of 98 valid species occurring in all zoogeographical regions, except Antarctica. Seven species occur in the Afrotropics, recorded from Cameroon, Democratic Republic of Congo, Ethiopia, Madagascar, Mozambique, South Africa and Yemen. *Calycomyza* is a moderately diverse genus of leaf-miners that is best represented in the New World (Spencer & Steyskal 1986: 140), particularly the Neotropics (Boucher 2010). The Old World is relatively depauperate in species, represented by only 12 species, including the relatively widespread *C. humeralis* (von Roser, 1840) and *C. solidaginis*, both of which extend into the Afrotropics. The Afrotropical fauna is further represented by the endemic *C. gigantissima* Spencer, 1959 and *C. malagasica* Černý, 2010 and the introduced *C. eupatorivora* and *C. lantanae*. The genus is readily distinguished from similar Phytomyzinae genera in having only two dorsocentral setae (sometimes with a slightly enlarged setula in front of the second dorsocentral seta, rarely with four well-developed dorsocentral setae), thick patches of tubercle-like setae on the surstylus and epandrium (Fig. 37) and for most species, characteristic black colouration, with the notopleuron and head pale yellow, excluding the antenna and sometimes the orbital plate. *Liriomyza*



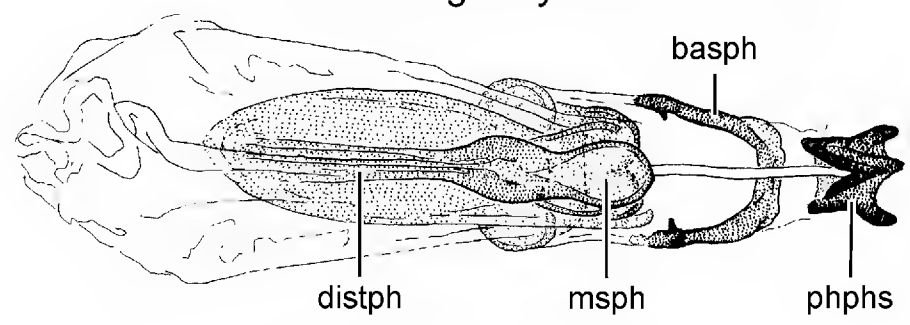
53 *Ophiomyia* ♂



54 *Ophiomyia* ♂



55 *Melanagromyza* ♂



56 *Melanagromyza* ♂

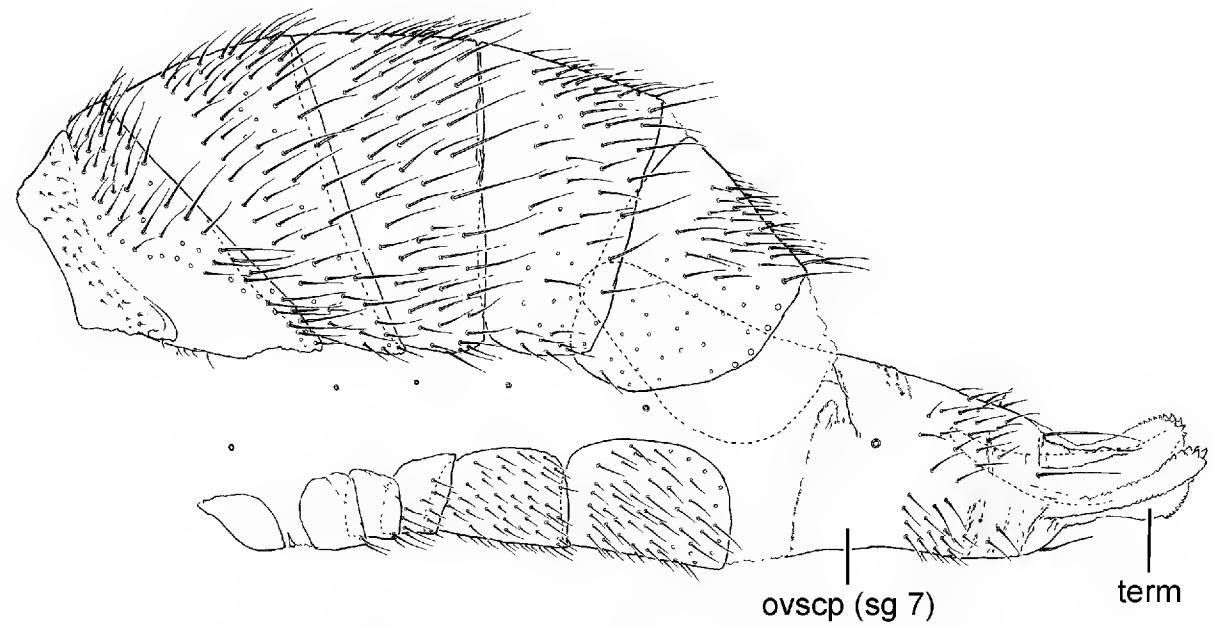
Figs 86.53–56. Male terminalia (phallus) of Agromyzidae (Agromyzinae): (53) *Ophiomyia phaseoli* (Tryon), lateral view; (54) same, ventral view; (55) *Melanagromyza vernoniana* Steyskal (non-Afrotropical), lateral view; (56) same, ventral. Figs 53, 54 (Lonsdale 2014, figs 17, 16, respectively).

Abbreviations: basph – basiphallus; distph – distiphallus; msph – mesophallus; phphs – phallophorus.

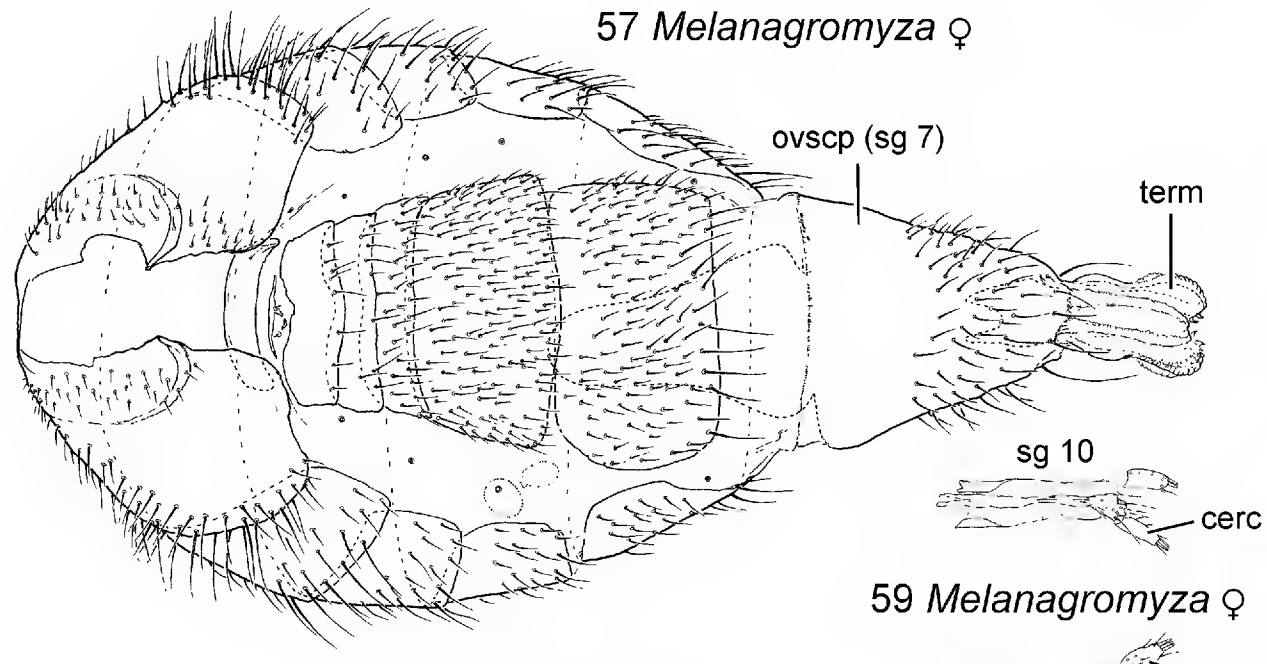
species have similar colouration, but these often have a medial yellow fascia on the scutellum and paler antennae. Some *Cerodontha* (*Poemyza*) species have the anterior two pairs of dorsocentral setae moderately to strongly reduced and some also have similar colouration, but in these species the frons is deeply emarginate anteromedially.

***Cerodontha* Rondani** (Phytomyzinae)**.** A genus of 295 valid species occurring in all zoogeographical regions, except Antarctica. Twenty-one species occur in the Afrotropics, recorded from the continental Afrotropics, the Arabian Peninsula, Cabo Verde, Madagascar and Seychelles. Aside from a relatively large lunule (Fig. 10), Afrotropical species of this widespread genus are further characterised by a dark, elongate, bifid distiphallus (a single tubule occurs in the Holarctic/Oriental subgenus *C.* (*Xenophytomyza* Frey), although three new species in the subgenus *C.* (*Icteromyza*) from Zimbabwe and Uganda have extremely short, atypical phalli without tubules). Seven valid subgenera of *Cerodontha* are recognised globally, with the relative dimensions of the lunule forming the primary basis upon which the genus is divided. The valid Afrotropical fauna is divided as follows: *Cerodontha sensu stricto* (7 species); *C.* (*Butomomyza*) (4); *C.* (*Dizygomyza*) (1); *C.* (*Icteromyza*) (3); and *C.* (*Poemyza*) (6). The remaining subgenera, namely: *C.* (*Phytagromyza* Hendel) and *C.* (*Xenophytomyza*) are not recorded from the region. *Cerodontha* species are entirely monocotyledon-feeders in the Cyperaceae, Iridaceae, Juncaceae, Poaceae and Tofieldiaceae and some species may be quite regionally abundant, especially those of the subgenus *Cerodontha sensu stricto*. Several *C.* (*Dizygomyza*) and *C.* (*Poemyza*) species possess a stridulatory file on the abdominal pleuron, similar to that of many *Liriomyza*, but is shorter, wider and flatter.

***Haplopeodes* Steyskal** (Phytomyzinae)**.** A genus of 17 valid species occurring in the Afrotropical, Nearctic and Neotropical Regions. This peculiar genus is represented in the Afrotropics



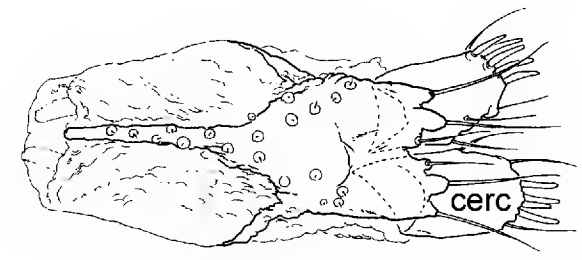
57 *Melanagromyza* ♀



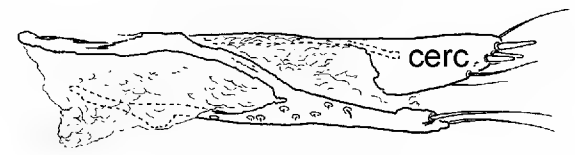
58 *Melanagromyza* ♀

59 *Melanagromyza* ♀

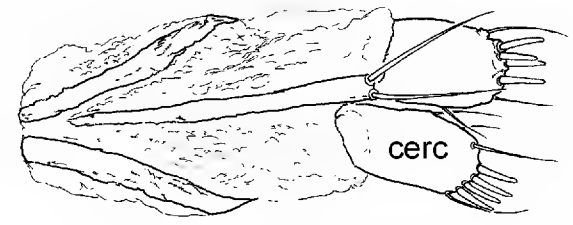
60 *Melanagromyza* ♀



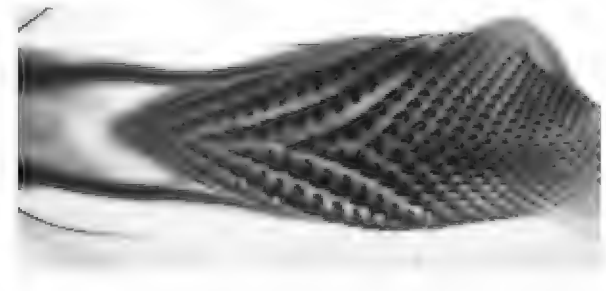
61 *Phytomyza* (*Phytomyza*) ♀



62 *Phytomyza* (*Phytomyza*) ♀



63 *Phytomyza* (*Phytomyza*) ♀



64 *Phytomyza* (*Phytomyza*) ♀

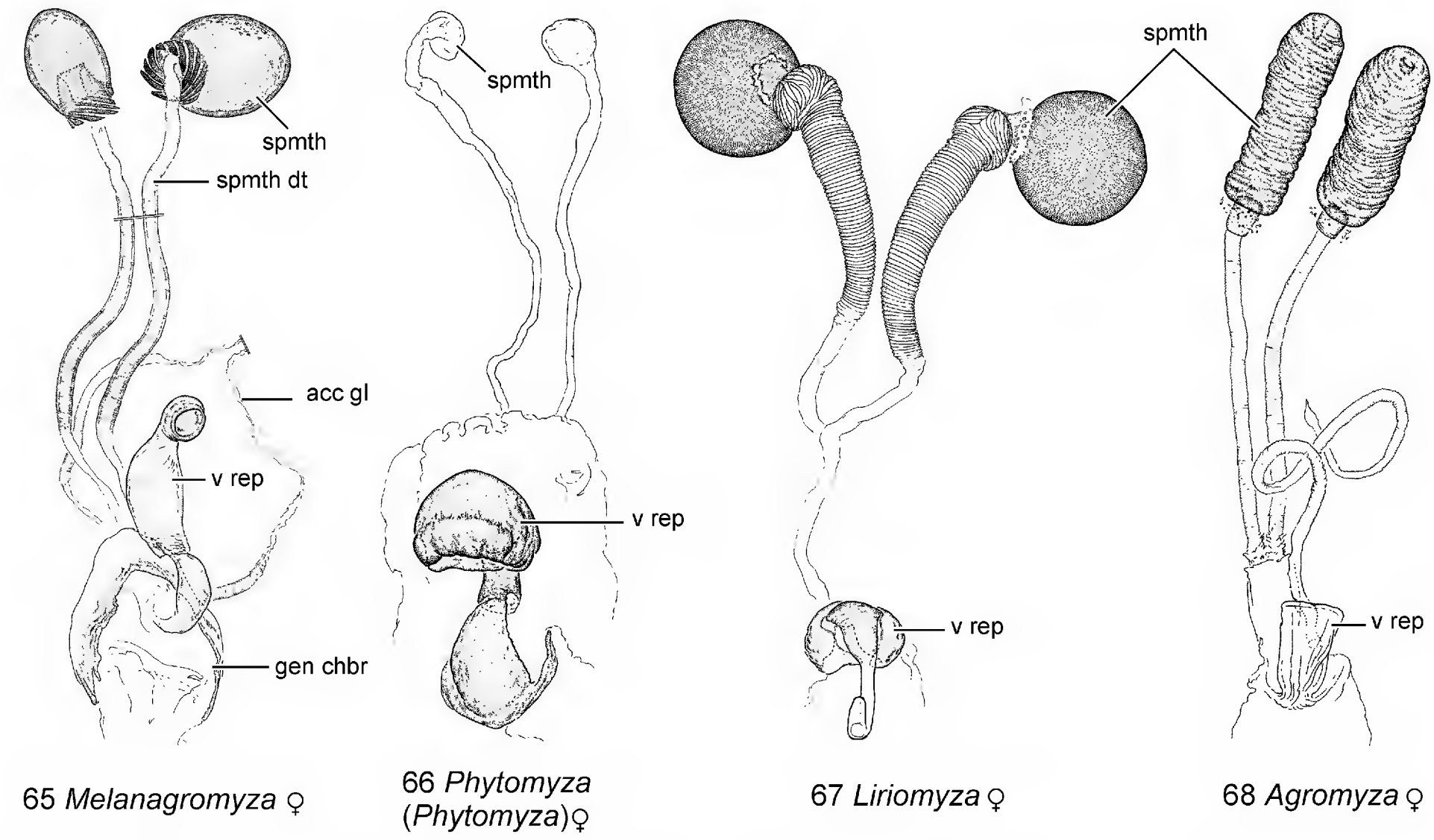
Figs 86.57–64. Female abdomen and terminalia of Agromyzidae: (57) abdomen (with terminalia retracted) of *Melanagromyza metallica* (Thomson), lateral view; (58) same, ventral view; (59) segment 10 to cercus of *M. metallica*, ventral view; (60) same, dorsal view; (61) same, *Phytomyza* (*Phytomyza*) *horticola* Goureau, ventral view; (62) same, lateral view; (63) same, dorsal view; (64) denticles on membrane anterior to segment 8 of *P.* (*Ph.*) *flavofemorata* Strobl, ventral view (non-Afrotropical).

Abbreviations: cerc – cercus; ovscp – oviscape; sg – segment; term – terminalia.

by the single species, *H. diminuella* (Spencer, 1961), from South Africa. Considering that this species is known only from a single female and the genus is otherwise known only from the New World, it is highly likely that this species is actually *Liriomyza*, which is sometimes highly similar in appearance. Aside from relatively pale colouration and a matt grey scutum, species are characterised by reduction, including reduced size, frequent loss of wing crossvein *dm–m*, no stridulating mechanism, a simplified and largely membranous phallus, a thin ejaculatory apodeme with little pigment on the basal bulb and a general reduction in chaetotaxy, including only one reclinate upper fronto-orbital seta (less commonly two) and reduced fronto-orbital and notal setulae. Larvae produce linear or blotch mines in Amaranthaceae, Chenopodiaceae, Portulacaceae and Solanaceae.

***Japanagromyza* Sasakawa** (Agromyzinae)**.** A genus of 83 valid species, occurring in all zoogeographical regions, except Antarctica, with most species occurring in the tropics. Seven species are recorded from the Afrotropics that are widely distributed in the continental Afrotropics and in Seychelles. *Japanagromyza* is a morphologically variable group. The Afrotropical fauna was treated by Lonsdale (2013), including one unnamed South African species known only from females, although the diversity of the genus is certainly much greater. Species have a prescutellar acrostichal seta and/or a lateromedial seta on the fore tibia and a small comb of setae on the inner distal surface of the hind tibia. Numerous species also have an entirely to mostly brown halter, a metallic shine on the thorax and abdomen (frequently confusing it for species of *Melanagromyza* that may also have a posterolateral seta on the fore tibia – see identification key above), often two well-developed dorsocentral setae (sometimes three, rarely four (*J. rutiliceps* (Melander, 1913)) and a characteristic frons that is relatively smooth and rounded, with a narrow, unraised orbital plate; the male terminalia, particularly the phallus, is highly diagnostic and sometimes elaborate at the species-level (as in Figs 51, 52). Larvae are blotch leaf-miners and 14 species occur on legumes, including the only Afrotropical species for which host data are available, *i.e.*, *J. parvula* Spencer, 1961 (*Crotalaria* L.). The Palaearctic *J. salicifolii* (Collin, 1911), which extends into temperate North Africa, is a leaf-miner of Salicaceae. Lonsdale (2013) provided an identification key to Afrotropical species.

***Liriomyza* Mik** (Phytomyzinae)**.** A mostly north temperate genus of 453 valid species occurring in all zoogeographical regions, except Antarctica. Ninteen species are recorded in the continental Afrotropics, the Arabian Peninsula, Cabo Verde, Madagascar, Mauritius, Mayotte Is., Réunion Is. and Seychelles, but these likely represent a small proportion of the actual fauna. *Liriomyza* belongs to a complex of highly similar genera that often overlap in external appearance, likely due to non-monophyly amongst groups, thereby regularly necessitating examination of the male terminalia for confident generic



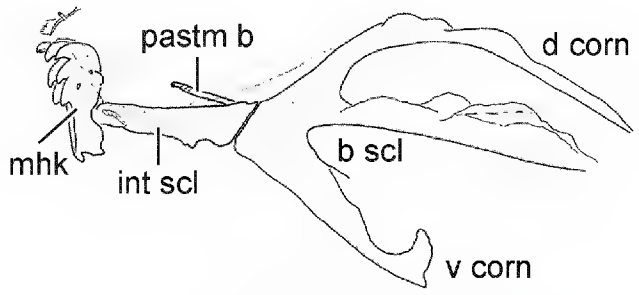
65 *Melanagromyza* ♀ 66 *Phytomyza* (*Phytomyza*)♀ 67 *Liriomyza* ♀ 68 *Agromyza* ♀

Figs 86.65–68. Female abdomen and terminalia of Agromyzidae: (65) internal terminalia of *Melanagromyza metallica* (Thomson), ventral view; (66) same, *Phytomyza* (*Phytomyza*) *horticola* Goureau; (67) same, *Liriomyza sativae* Blanchard; (68) same, *Agromyza* sp.

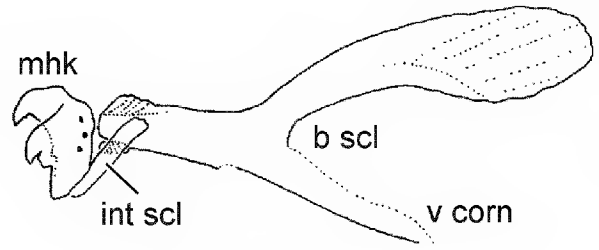
Abbreviations: acc gl – accessory gland; gen chbr – genital chamber; spmth – spermatheca/e; spmth dt – spermathecal duct; v rep – ventral receptacle.

69 *Phytomyza* (*Phytomyza*)

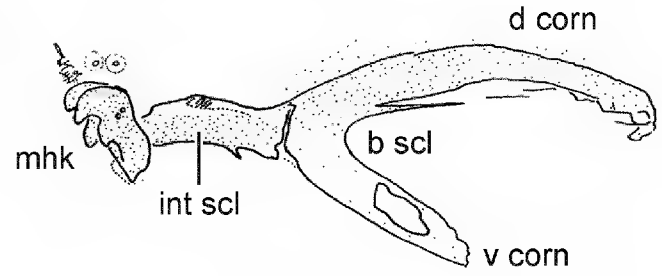
70 *Phytomyza* (*Phytomyza*)



71 *Agromyza*

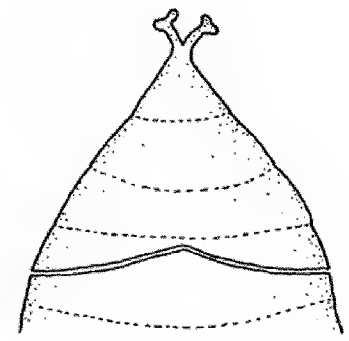


72 *Liriomyza*

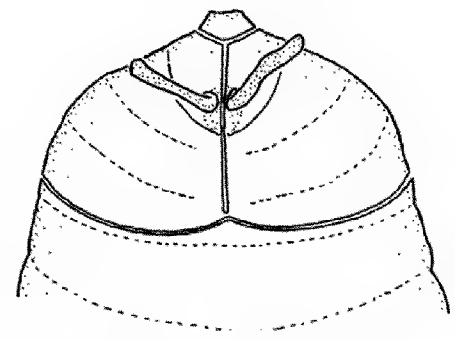


73 *Phytomyza* (*Phytomyza*)

74 *Phytomyza* (*Phytomyza*)



77 *Phytomyza* (*Phytomyza*)

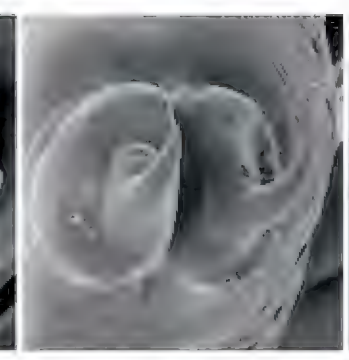


78 *Tropicomyia*

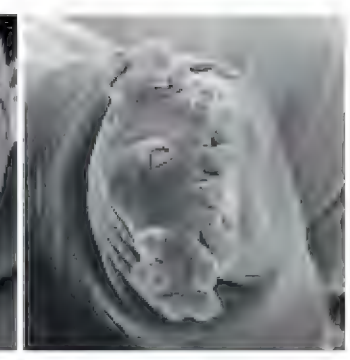
75 *Phytomyza* (*Phytomyza*)

76 *Phytomyza* (*Phytomyza*)

79 *Agromyza*



80 *Melanagromyza*



81 *Phytomyza* (*Phytomyza*)

Figs 86.69–81. Immature stages of Agromyzidae: (69) larval habitus of *Phytomyza* (*Phytomyza*) *chelonei* Spencer, lateral view (non-Afrotropical); (70) same, anteroventral view; (71) larval cephaloskeleton of *Agromyza anthracina* Meigen, lateral view (non-Afrotropical); (72) same, *Liriomyza pusilla* (Meigen) (non-Afrotropical); (73) same, *Ph.* (*Ph.*) *horticola* Goureau; (74) puparium of *Ph.* (*Ph.*) *misella* Spencer, lateral view (non-Afrotropical); (75) same, anterior view; (76) same, caudal view; (77) anterior end of puparium of *Ph.* (*Ph.*) *milii* Kaltenbach, dorsal view (non-Afrotropical); (78) same, *Tropicomyia* theae (Cotes); (79) puparial posterior spiracles of *Agromyza albipennis* Meigen, caudal view (non-Afrotropical); (80) same, *Melanagromyza lappae* Loew (non-Afrotropical); (81) same, *Ph.* (*Ph.*) *ranunculi* (Schrank). Figs 71–73, 77–81 (Dempewolf 2001, figs 48, 239, 368, 29, 31, 22, 23, 25, respectively).

Abbreviations: b scl – basal sclerite; d corn – dorsal cornu; int scl – intermediate sclerite; mhk – mouthhook; pastm b – parastomal bar; v corn – ventral cornu.

placement. As currently delimited, a pigmented and apically swollen ejaculatory duct (Figs 27–34) and decoupling of the surstylus and subepandrial sclerite are the only features consistently reliable for genus-level placement (Lonsdale 2011; Zlobin 1997). Other features often useful for diagnosis include a dark notum with a yellow notopleuron and a yellow medial fascia on the scutellum (Figs 2, 3), a reduced connection between the postgonite and epiphallus and often only one or two spines on the surstylus and epandrium, but there are exceptions and similar states found in other genera; a male stridulatory file is sometimes also present on the anterolateral abdominal membrane (Figs 3, 4). *Liriomyza* feed on eight families of monocotyledons (Alliaceae, Asparagaceae, Commelinaceae, Hemerocallidaceae, Juncaginaceae, Liliaceae, Melanthiaceae and Poaceae) and 42 families of dicotyledons and four species occur on Equisetaceae (Benavent-Corai *et al*. 2005; Spencer 1990: 4). Most are leaf-miners, but a minority feed in seeds and stems (Spencer & Steyskal 1986: 107). Some species are polyphagous, including the agriculturally significant species discussed above, but most *Liriomyza* appear to have a more limited host range, recorded from only one host species or genus.

***Melanagromyza* Hendel** (Agromyzinae)**.** A genus of 380 valid species occurring in all zoogeographical regions, except Antarctica. Ninty-six species occur in the Afrotropics, in almost all Afrotropical countries; the genus being virtually cosmopolitan. Species of *Melanagromyza* are the dominant agromyzid faunal element in the New (Boucher 2010: 1069) and Old World tropics (Spencer 1959), in terms of both individuals and species richness. Species often have a metallic sheen on the abdomen and thorax (also some *Japanagromyza* and *Ophiomyia*), the halter is black and most species have dorsally pilose eyes (Fig. 6) (similar genera have bare eyes, or very short, sparse microtrichia), two dorsocentral setae, posteromedial setae on the mid tibia and (less commonly) the fore tibia and a central horn on the hind larval spiracle (Fig. 80). The costal vein (*C*) extends to vein M_1, but in a minority of species the costal vein is shortened (e.g., the Afrotropical *M. curiosa* Spencer, 1959 and *M. cyrtanthi* Spencer, 1960). The male terminalia are most definitive of the genus: the basiphallus is short, symmetrical and U-shaped, or ring-like (Figs 55, 56); the ventral margin of the epandrium is often produced into a small spine (also some *Tropicomyia*); and the ventrobasal surface of the distiphallus has one pair of thin tubules flanking the mesophallus. Species are almost entirely miners/borers in stems (Fig. 83), seeds, roots and flower heads, but a few species are known to mine leaves, including the Afrotropical *M. cyrtorchidis* Spencer, 1985. A minority of stem-miners also induce a swelling, or "gall", including the South African *M. gymnosporivora* Spencer, 1963. A peculiar substrate for the larva of *M. acaciae* Spencer, 1963, is the ubiquitous swollen thorn galls of "whistle trees" in the Afrotropical savannas produced and inhabited by ants (Hocking 1971).

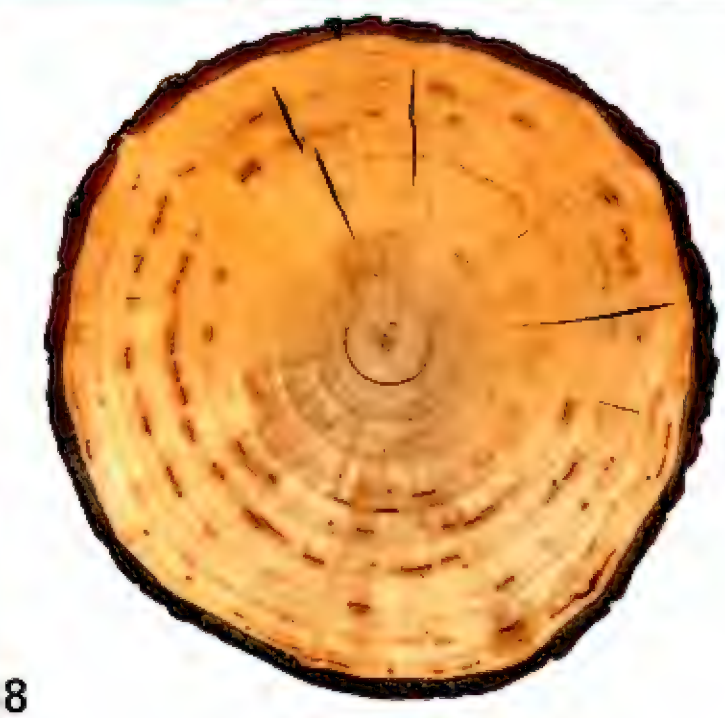
***Metopomyza* Enderlein** (Phytomyzinae)**.** A genus of 21 valid species occurring in the Afrotropical, Nearctic, Oriental and Palaearctic Regions. *Metopomyza* is here reported from the Afrotropics for the first time, with an undescribed species close to *M. scutellata* (Fallén, 1823) collected at Mt Kilimandjaro in Tanzania (M. von Tschirnhaus, pers. obs.). Species are otherwise known from north temperate regions south to Nepal (Sasakawa 1996; Zlobin 2003*b*). Adults are here characterised as being mostly dark in colouration, with a centrally yellow scutellum and a brown orbital plate. The orbital plates are slightly to strongly pronounced, distinct from the softer medial portion of the frons that is sometimes also brown and they form the shape of an "M" with the heavily sclerotised ocellar triangle; the intervening angles in the "M" are sharp, not rounded or otherwise broad. The Palaearctic genus *Selachops* is the most likely sister genus, sharing highly similar male terminalia: epandrium with two saw-like lines of tubercles on inner surface; subepandrial sclerite bare; phallus bifid with paraphallus pronounced. The larvae of *Metopomyza* species are leaf-miners in Cyperaceae, Juncaceae and Poaceae.

***Ophiomyia* Braschnikov** (Agromyzinae). A genus of 324 valid species occurring in all zoogeographical regions, except Antarctica. Forty-five species occur in the continental Afrotropics, the Arabian Peninsula, Cabo Verde, Madagascar, Mauritius and Réunion Is. *Ophiomyia* is one of the most speciose and commonly encountered Afrotropical Agromyzinae after *Melanagromyza*. Morphological diversity is pronounced, but with few exceptions, species can be readily diagnosed by the clypeus, which is truncated (not rounded) anteriorly (Figs 7, 8). A few *Melanagromyza* also have a somewhat truncated clypeus, but in these few species the anterior margin is usually without corners and there is a suite of additional derived features otherwise characteristic of that genus, suggesting that this state is independently derived. One large lineage of *Ophiomyia* is quite readily identified, exhibiting a facial keel that usually has a medial swelling and a gena that is often angled or produced anteriorly (sometimes strikingly so), with males also often exhibiting a horn of clustered vibrissae at the apex called a "fasciculus" (Fig. 8). The definition and generic boundaries of *Ophiomyia* have been quite varied historically. The most recent treatment by Lonsdale (2014), discussed above, outlined a relatively inclusive definition of the genus, encompassing the small and unusual genera *Kleinschmidtimyia* Spencer and *Penetagromyza* Spencer and some polyphyletic *Hexomyza* Enderlein. Species of *Penetagromyza* are Afrotropical *Aloe*-miners that usually lack postocellar setae and have a costal wing vein that extends to vein R_{4+5}; the former *Kleinschmidtimyia* is an Old World, mostly tropical lineage of minute leaf-miners with a white calypter, three inclinate anterior fronto-orbital setae and one reclinate posterior fronto-orbital seta, bare tibiae, a characteristic phallus and serrate larval mouthhooks. Larval habits are varied, including stem-miners, root-borers, seed-miners, leaf-miners and gall-formers. Stem-borers feed and pupariate close to the stem surface, not deep within it, as do *Melanagromyza*. Dicotyledons are the usual host-plants for *Ophiomyia* species, although several species develop in the monocotyledon genera *Aloe* (Asphodelaceae), *Asparagus* (Asparagaceae) and *Hemerocallis* (Asphodelaceae).

***Phytobia* Lioy** (Phytomyzinae)**.** A genus of 117 valid species occurring in all zoogeographical regions, except Antarctica. Seven Afrotropical species are recorded from Malawi, Nigeria, Rwanda, Sierra Leone and South Africa. Additional collecting should increase known species diversity considerably, as unpublished records already exist from Cabo Verde, Central African Republic and Somalia, with rainforests being particularly rich (M. von Tschirnhaus, pers. obs.). Six species were listed by Cogan (1980: 646) and two species were described by Zlobin

(2007), but Spencer's (1961*a*) identification of *P. nigrita* (Malloch, 1914) was later considered doubtful and deferred until males could be examined (Spencer 1965). Adults are relatively large (wing length: 3–5 mm), although *P. gigas* Spencer, 1966, reaches 6.5 mm (Spencer 1966); vein R_{4+5} is at least as close to the wing tip as vein M_1 (Fig. 13); the lunule is pubescent to silvery; and in many species the phallus is long and thin, with a narrow hypophallus and a straight, thin mesophallus fused to the distiphallus (Figs 43, 44). The unusual damage caused by larvae in trees as they mine in xylem are termed "pith flecks" (Fig. 88); no other insects, including Buprestidae (Coleoptera) and microlepidoptera are known to produce these specific semicircular tunnels that have regular right and left blind offshoots (Fig. 87; Tschirnhaus (1992, plate 13)). Consequently, a number of *Phytobia* host and geographic records have accumulated in the literature on the basis of this characteristic damage alone (Spencer 1990: 18) and await confirmation from larval rearings and adult collection.

Phytoliriomyza **Hendel** (Phytomyzinae)**.** A genus of 114 valid species occurring in all zoogeographical regions, except Antarctica. Seven species occur in the Afrotropics, distributed



Figs 86.82–88. Examples of Agromyzidae feeding traces on host-plants: (82) *Euhexomyza schineri* (Giraud) gall on *Populus* (non-Afrotropical); (83) *Melanagromyza sojae* (Zehntner) stem mine (with larva) in *Glycine max* (L.) (Soybean) (non-Afrotropical); (84) *Ophiomyia camarae* Spencer, leaf mine on *Lantana*; (85) *Pseudonapomyza* sp. leaf mine on *Tecoma*; (86) indet. Agromyzidae leaf mine on plant (non-Afrotropical); (87) *Phytobia cambii* (Hendel) mines under bark of *Betula* (non-Afrotropical); (88) cross-section of *Salix* with "pith flecks" caused by *P. cambii* mining in xylem. Fig. 82 (photograph © T. Murray), Fig. 83 (photograph © M. Shepard, G.R. Carner and P.A.C. Ooi), Fig. 84 (photograph © ARC-PPRI, South Africa).

in Cabo Verde, Kenya, Lesotho, Madagascar, Namibia, Oman, South Africa, Tanzania and Yemen (Černý & Tschirnhaus 2014). Many species have a characteristic light velvety covering of brown and/or grey pruinosity across the body, that is sometimes slightly patterned on the thorax and is often whitish or silvery on the head, being particularly reflective on the orbital plate; some of these also have an apically brown halter and proclinate or absent fronto-orbital setulae and some have the centre of the scutellum yellowish. Numerous other species have a scutellum that is distinctly yellow medially and are externally indistinguishable from *Liriomyza*, although some have a strikingly black antennal postpedicel and most have discrete rows of tubercles on the inner surface of the epandrium, similar to those of *Metopomyza*. Some also have an apically swollen ejaculatory duct, but unlike *Liriomyza*, this is devoid of pigment. The genus is quite heterogeneous in morphology and host preference and is unlikely to be monophyletic. Larvae of *Phytoliriomyza* mine in the leaves and stems of various angiosperms and ferns and are the only Agromyzidae known from liverworts (Hering 1957, 1966; Spencer 1990: 1).

***Phytomyza* Fallén** (Phytomyzinae)**.** A genus of 774 valid species occurring in all zoogeographical regions, except Antarctica. Thirty-three species occur in the Afrotropics, distributed in the continental Afrotropics, Cabo Verde, Madagascar and Yemen. *Phytomyza* is likely the largest and most diverse genus of Agromyzidae, with all species diagnosed by proclinate fronto-orbital setulae (Fig. 9), a costal vein only extending to vein R_{4+5} (Figs 17, 18), a weak/spectral M_1 vein and the absent or basally situated crossvein *dm–m*. All valid subgenera of *Phytomyza* occur in the Afrotropics, *i.e.*, *Phytomyza sensu stricto*, *P.* (*Napomyza*) and *P.* (*Ptochomyza*). Zlobin (1994) redefined *P.* (*Napomyza*) to include only those species that have a longitudinal sclerotised strip on the dorsal margin of a membranous tubular distiphallus that connects to an apical sclerotised ring (Figs 35, 36), and have crossvein *dm–m* in line with crossvein *r–m* (not distal to *r–m*, as in other *Phytomyza* that have retained this crossvein). These species consist of "… stem, seed head and root feeders on Asteraceae and a few other (non-ranunculaceous) plants …" (Winkler *et al*. 2009: 269). The subgenus *P.* (*Ptochomyza*) is most reliably characterised by projecting orbits, a short second costal section (Fig. 18), reduced chaetotaxy and simplified terminalia; these species feed on *Asparagus* with one, *P.* (*Ptochomyza*) *mayeri* (Spencer, 1966), associated with *Clematis* (Ranunculaceae) (Spencer 1990: 29), and another, *P.* (*Ptochomyza*) *czernyi* Strobl, 1909, known from *Foeniculum* Mill. (Apicaeae) (Süss 2002). The host genera of *Phytomyza* listed in Benavent-Corai *et al*. (2005) belong to 63 botanical families, based on the classification of Mabberley (1997: 1). Species are primarily leaf-miners, but some occur in roots, stems, flower heads or seeds. Many are considered to be regionally pestiferous on one or several ornamental or food crops, but several species are highly polyphagous pests of global concern (see above).

***Pseudoliriomyza* Spencer** (Phytomyzinae)**.** A monotypic genus, with the single described species, *P. cordiae* (Spencer, 1959), described from Tanzania and later recorded from Java, Indonesia in the Oriental Region (Spencer 1966). The species is externally similar to *Liriomyza*, but has three rather than four dorsocentral setae, the intra-alar seta is absent, vein M_1 ends at the wing tip, the surstylus is absent, the epandrium has two rows of shallow unpigmented protuberances (Fig. 42), as in *Amauromyza*, the hypandrium is thick and broadly bowed (Fig. 41) and the ejaculatory apodeme has a large, bowl-like base. Based on the illustrations in Spencer (1966), the distiphallus consists of one pair of broad, pale tubules fused to an equally broad mesophallus (Figs 39, 40), also similar to some *Liriomyza*, but since this structure and the ejaculatory duct are missing from the original dissection, accurate phylogenetic placement of the genus cannot be established at this time.

***Pseudonapomyza* Hendel** (Phytomyzinae)**.** A genus of 102 valid species occurring in all zoogeographical regions, except Antarctica. Of the thirty-seven species described from the Afrotropics, 24 are endemic to the region, distributed throughout the continental Afrotropics, the Arabian Peninsula, Cabo Verde, Madagascar and Mauritius. Numerous additional undescribed species are also known from across the continental Afrotropics. Most *Pseudonapomyza*, globally and in the Afrotropics, belong to the widespread Poaceae-feeding *P. atra*-group, characterised by the angulate antennal postpedicel (exception *P. ovalis* Zlobin, 2002, from Tanzania), absence of wing crossvein *dm–m* (Fig. 16) and crossvein *r–m* almost adjacent to crossvein *bm–m* (Černý 2008; Zlobin 2003*a*). The few remaining species belong to the *P. acanthacearum*-group (Zlobin 2003*a*), known from the Afrotropical, Australasian and Oriental Regions, but additional material is also known from the temperate Neotropics (M. von Tschirnhaus, pers. obs.). Species in this group, which are mostly leaf-miners in Acanthaceae, but also Amaranthaceae, Asteraceae (Černý 2008) and Bignoniaceae (Madire *et al*. 2011*a*, *b*), have retained crossvein *dm–m* (which is often basal to crossvein *r–m* (Fig. 15), but is sometimes distal to *r–m*, similar to *Aulagromyza*) and a rounded antennal postpedicel. Some species also possess a prescutellar acrostichal seta, bicolored halteres and one, two or rarely 3–5 posterolateral setae on the mid tibia. Both species-groups are further characterised by small body size, dark colouration (tibiae partly ochrous, tarsi partly yellowish), costalisation of the radial veins, vein M_1 faded or reduced to a light fold, the costal vein (C) extending to vein R_{4+5}, fronto-orbital setulae erect to reclinate (sometimes absent) and often a characteristically shaped meso- and distiphallus (Figs 45, 46). Several species belonging in the *P. atra*-group have been reported attacking maize, the larvae and puparia being easily identified by bands of black spinules around the body.

***Tropicomyia* Spencer** (Agromyzinae)**.** A genus of 37 valid species occurring in the Afrotropical and Australasian/Oceanian Regions. Twenty species occur in the Afrotropics, recorded throughout the continental Afrotropics, Cabo Verde, Madagascar, Mauritius and Rodrigues Is. *Tropicomyia* comprises mostly minute (wing length: 1.2–2.3 mm), almost uniformly dark species, without a metallic sheen, that mostly occur in the Old World tropics and Japan. Five species of economic concern are unusually polyphagous, including the Afrotropical *T. flacourthiae* (Figs 49, 50) (see above). The genus, as currently conceived, is likely non-monophyletic, although most species can be readily assigned to a well-characterised lineage containing in part what previous authors have treated as "*Tropicomyia sensu stricto*", partially defined by serrated larval mouthhooks adapted to feeding on soft epidermal cells without chloroplasts. Lonsdale (2014) noted that these species are part of a larger grouping, mostly characterised by terminalic synapomorphies

that likely define the actual boundaries of the genus, including a unique male distiphallus, a pair of projecting lateral plates on a U-shaped basiphallus and the lack of stout or tubercle-like setae on the surstylus. These species also have four fronto-orbital setae, with only the anterior seta strongly incurved, a very shallow gena, 0–1 reduced medial tibial seta, a short penultimate section of vein M_1 (*i*.e., between the crossveins) and hind spiracles standing on a narrowed elongate extension of the puparium.

Undescribed genus (Agromyzinae)**.** An endemic genus of four undescribed species, three from Kakamega Forest (Kenya) and one from Kanyanchu (Uganda) (M. von Tschirnhaus, unpubl.). The genus is characterised as follows: body brown, without metallic sheen; halter white; face flat, without medial keel; lunule distinctly lower than a semicircle; ocellar triangle absent; clypeus narrow and rounded; fronto-orbital setulae absent or reclinate; one male vibrissa; eye of both sexes bare; posterior intra-alar present; prescutellar acrostichal present in three species; 3 + 1 dorsocentral setae; wing typical of subfamily; costal vein extending to vein R_{4+5} or vein M_1; two postero-dorsal setae on mid-tibia; apex of distiphallus mostly indistinct, hyaline, with dark, elongate supporting sclerites; epandrium of two species with a pair of acute black hook-like appendices pointing upwards or caudally; and surstyli separate from epandrium. Biology and immature stages remain unknown.

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ANTHOMYZIDAE 87

(Anthomyzid Flies)

Jindřich Roháček

Fig. 87.1. Female of *Amygdalops thomasseti* Lamb (Turkey) (photograph © J. Roháček).

Diagnosis

Small-sized (body length: 1.3–4.5 mm), slender to very slender acalyptrate flies (Figs 1–3, 6, 13, 14), with relatively short legs; wings (if present) usually long and narrow (Figs 20–26); body variable in colour, yellow to black, sometimes with dark or pale vittae or maculae, distinctly micro-tomentose to largely bare and lustrous.

Head (Figs 4, 5, 7–11) as wide as, or wider than thorax, rounded to angular in profile, sometimes with frons projecting; frons usually broad, slightly tapered anteriorly, in some groups narrower (Fig. 5); compound eye and ocellar triangle well-developed; frontal triangle usually distinct; interfrontal area often slightly depressed; occiput dorsally slightly to distinctly concave (Figs 4, 5); face medially depressed and weakly sclerotised; parafacial narrow; gena narrow, $< 1/5$ eye height; head chaetotaxy (Figs 5, 7, 9, 10): postvertical setae small, convergent to cruciate, rarely absent, situated behind ocellar triangle (Figs 4, 5); outer and inner vertical setae and ocellar seta usually strong; 1–3 reclinate fronto-orbital setae (anterior usually shorter) and 0–2 setulae in front of anterior fronto-orbital seta; single row of subvibrissal and postocular setulae (doubled postocular setulae only in fossil *Protanthomyza* Hennig); 1 long vibrissa and 1 shorter anterior subvibrissal seta (latter sometimes reduced); compound eye large, usually almost bare

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2021. Manual of Afrotropical Diptera. Volume 3. Brachycera—Cyclorrhapha, excluding Calyptratae. *Suricata* 8. South African National Biodiversity Institute, Pretoria; pp. 1939–1956.

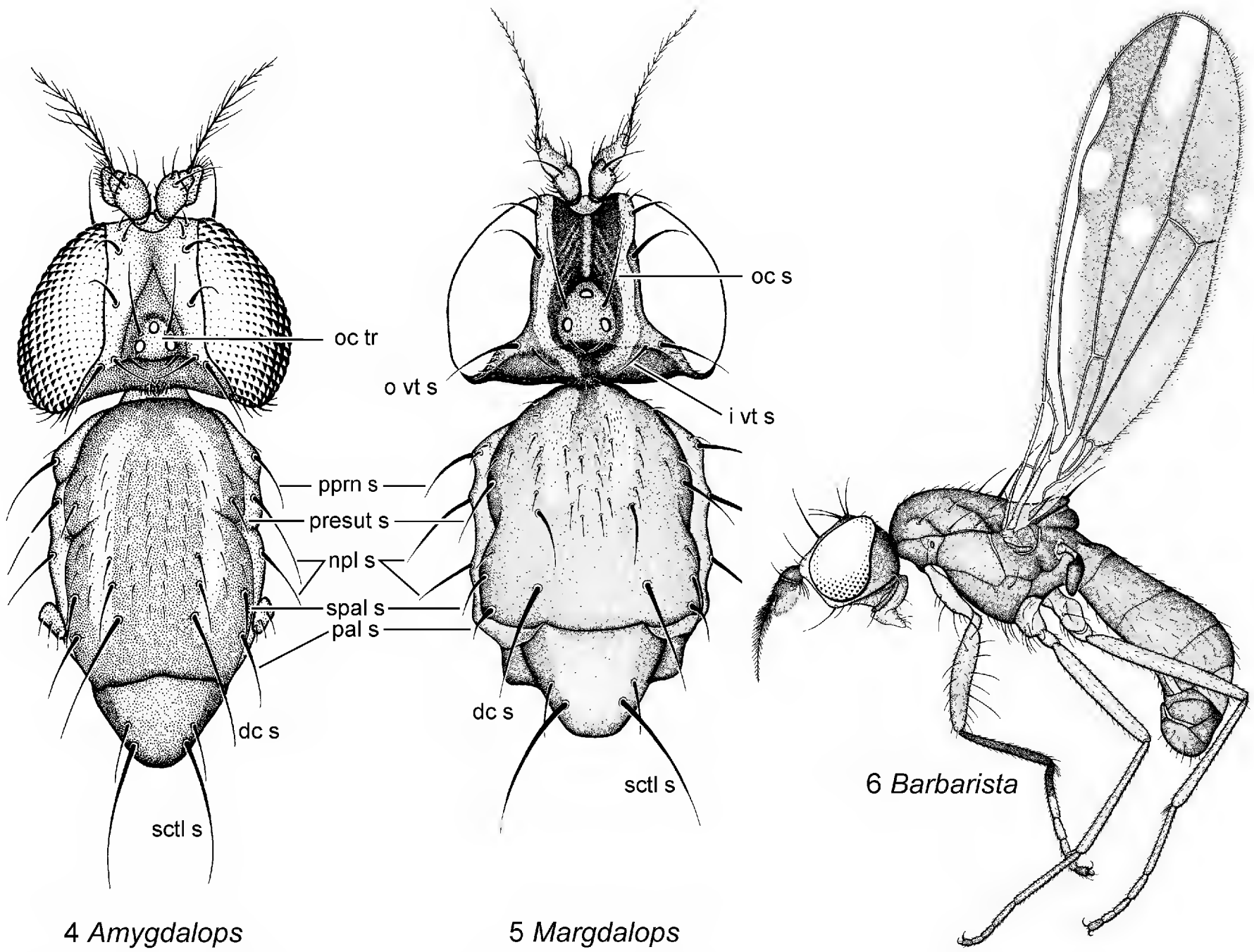
(finely setulose in *Zealantha* Roháček), oval to irregularly subovoid, with longest diameter oblique to vertical; antenna short, usually geniculate between pedicel and postpedicel (Figs 7, 9, 10), porrect in fossil *Protanthomyza* and some recent genera (e.g., Afrotropical *Amnonthomyza* Roháček and *Barbarista* Roháček, see Figs 8, 11, 12); postpedicel laterally flattened, apically rounded, ciliate, rarely with long pale setae (*Scelomyza* Séguy, Fig. 9); arista short-ciliate to long-pectinate, inserted dorsally, mid-length to proximally; clypeus relatively small; proboscis usually short, labella moderate and fleshy; palpus slender, usually with 1 longer seta besides small setulae.

Thorax (Figs 4, 5, 13, 14), with postpronotal lobe well-developed; mesonotum with transverse suture distinct laterally; thoracic chaetotaxy (Figs 4, 5): 1 postpronotal seta, 2 notopleural setae, 0–1 presutural intra-alar seta, 0–1 supra-alar seta, 1–2 postalar setae, 0–3 dorsocentral setae (all postsutural), becoming shorter anteriorly, 0–8 rows of acrostichal micro-setae, 2 pairs of (rarely 1, 3 or with some additional micro-setulae) scutellar setae, 1–2 (usually minute) proepisternal setae, 0 anepisternal setae (anepisternal macrosetae only in fossil *Protanthomyza*; micro-setae only in *Apterosepsis* Richards (Fig. 13) and one non-Afrotropical species of *Stiphrosoma* Czerny), 1–2 long katepisternal setae and several shorter setae ventrally; prosternum bare, wider anteriorly, not fused with propleuron; metasternum of moderate size, bare. Scutellum usually rounded, subtriangular, sometimes shortened; subscutellum usually distinct (large in some genera, see Fig. 6), rarely reduced (Fig. 13). Wing (Figs 20–26), long and narrow, rarely shortened or entirely absent (Figs 13, 14); membrane unicolourous or brown and white ornamented; costal vein (*C*) with 2 breaks or attenuations (humeral and subcostal breaks), reaching to apex of vein M_1, usually with small spinules among setulae between veins R_1 and R_{2+3} (Fig. 20); subcostal vein (*Sc*) (in extant taxa) weak, attenuated in apical $^1/_3$, fused with vein R_1 to form preapical kink on latter (Fig. 20), almost complete only in some fossil *Protanthomyza* species; vein R_{2+3} invariably long, curved to sinuate (except species with reduced wings); vein R_{4+5} usually straighter, subparallel with vein M_1 (Fig. 20); cells *bm* and *dm* sometimes incompletely separated; cells *dm* and *cua* usually closed (Fig. 20); vein *CuA+CuP* and often vein M_4 shortened, ending before wing margin; alula small, narrow; anal lobe sometimes strongly reduced and wing basally narrowed (Figs 25, 26); venation rarely reduced (some veins absent, e.g., in non-Afrotropical *Cercagnota* Roháček & Freidberg), particularly in brachypterous specimens (*Stiphrosoma*); halter well-developed, reduced only in short-winged forms, absent in apterous *Apterosepsis*. Legs short, slender, usually yellow, rarely dark variegated; fore femur with ctenidial spine (Figs 15, 18), secondarily lost in some groups (Fig. 19), rarely with thickened anteroventral setae (*Barbarista*, Fig. 16), besides usual rows of long posterodorsal and posteroventral setae; male with hind femur often armed with thickened and shortened posteroventral setae (Fig. 17); tibiae lacking dorsal preapical setae; mid tibia with distinct ventroapical seta; tarsomere 1 (hind in particular) sometimes with 1–3 short thickened ventrobasal setae.

Abdomen with pre-abdominal tergites large and broad, sternites usually small and narrow; male tergite 6 short, bare, often reduced or membranous; male sternites 6–8 more (6–7)

Figs 87.2–3. Photographs of living Afrotropical Anthomyzidae (both Tanzania): female of *Amygdalops* sp. near *poecilus* Roháček. Photographs © S.A. Marshall.

or less (8) asymmetrical, dorsally fused, situated left lateral to dorsal; male terminalia with epandrium (Figs 27, 28, 33, 34) semi-globular, with ventrally open anal fissure; cercus discrete (Figs 28, 33, 34); bacilliform (subepandrial) sclerite well-developed (Figs 28, 33, 34), sometimes setulose (usually on lateral arms); surstylus (Figs 27, 28, 30, 33, 34) separate, connected to bacilliform sclerite posteriorly; hypandrium (Figs 31, 32, 38, 39) frame-like, closed by posterior hypandrial bridge (Figs 29, 31, 38); pregonites (Figs 31, 32, 38, 39) fused with hypandrium; postgonites usually free (Figs 31, 32, 38, 39); phallic complex (Figs 29, 32) connected to hypandrium by "folding apparatus", formed by phallic part (Figs 32, 37), sclerotised caudal process (Figs 29, 32, 35, 36) of hypandrial bridge (may be absent), paired connecting sclerites (sometimes reduced) and basal membrane; phallapodeme (Figs 27, 29, 32, 37) with robust ventral phallic guide (fulcrum) that is ventrally attached to anterior connective of hypandrium (Figs 27, 32); phallus (Figs 29, 32, 37) composed of (usually short and frame-like) basiphallus and bifid distiphallus, formed by largely membranous saccus and slender sclerotised filum; ejaculatory apodeme very small (Figs 27, 29, 32, 37), often with slender digitiform process; female abdomen with tergites broader than male; postabdomen (Figs 40–42, 48, 49) with tergite and sternite 6 usually similar to those of segment 5; tergite and sternite 7 separate (sternite smaller, Figs 48, 49), or fused to form ring-shaped to conical syntergosternum 7 (Figs 40–42); tergite 8 small, of various shapes; sternite 8 either short-transverse or longer, often medially divided (Fig. 44), or with posteromedial cleft (Fig. 49); female genital chamber (Figs 43, 44, 46) usually with paired posterior internal sclerites and single medial annular sclerite (some or both may be reduced or rarely absent); anterior (distal) part of genital chamber with unpaired ventral receptacle (Figs 43, 46), often small, membranous or duct-like, but sometimes sclerotised and large, with vesicular accessory glands (1 + 1) on distally dilated, usually ringed ducts, arising near insertion of spermathecal ducts; spermathecae (1 + 1) globular (Figs 43, 45, 46) to elongate pyriform, with various surface structures; epiproct (supra-anal plate) small, with at



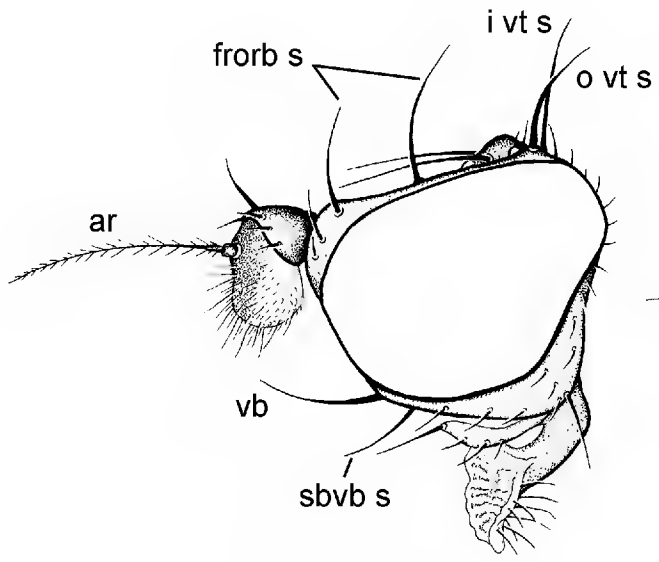
Figs 87.4–6. Heads and thoraces and habitus of Anthomyzidae: (4) head and thorax of *Amygdalops thomasseti* Lamb, dorsal view; (5) same, *Margdalops venustus* Roháček & Barraclough; (6) habitus of *Barbarista guttata* Roháček, lateral view. Fig. 4 (Roháček & Freidberg 1993, fig. 64), Fig. 5 (Roháček & Barraclough 2003, fig. 42), Fig. 6 (Roháček 1993, fig. 9).

Abbreviations: dc s – dorsocentral seta; i vt s – inner vertical seta; npl s – notopleural seta; o vt s – outer vertical seta; oc s – ocellar seta; oc tr – ocellar triangle; pal s – postalar seta; pprn s – postpronotal seta; presut s – presutural seta; sctl s – scutellar seta; spal s – supra-alar seta.

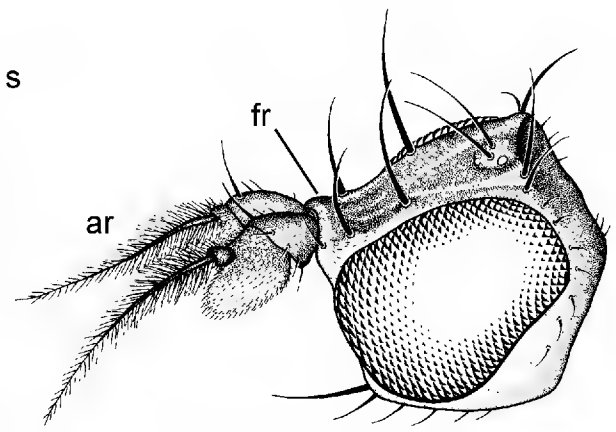
least 1 pair of long setae; hypoproct (sub-anal plate) usually larger than epiproct, simple, rarely modified; cercus usually discrete, with rich setosity (Figs 40–42, 48, 49).

Egg (Figs 50, 51) colour whitish to dirty yellow; relatively voluminous (length: 0.6–1.0 mm; width: 0.17–0.30 mm), shape elongate cylindrical to casket-like, with tapered ends; dorsal surface more convex than ventral; micropore situated on ventral side of more produced anterior end; chorion differently formed on ventral (fine reticulate micro-sculpture or smooth) and dorsal (longitudinal furrows, ribs or bands) sides; in Afrotropical *Barbarista* ventral side unusual with fine, zig-zag pattern (Fig. 50). For described eggs see Roháček (1986, 1992, 1993), Roháček & Báez (1988), Roháček & Barber (2011) and Roháček & Freidberg (1993), but note that in all previous descriptions and illustrations, except Roháček & Barber (2011), dorsal egg surface misinterpreted as ventral and *vice versa*.

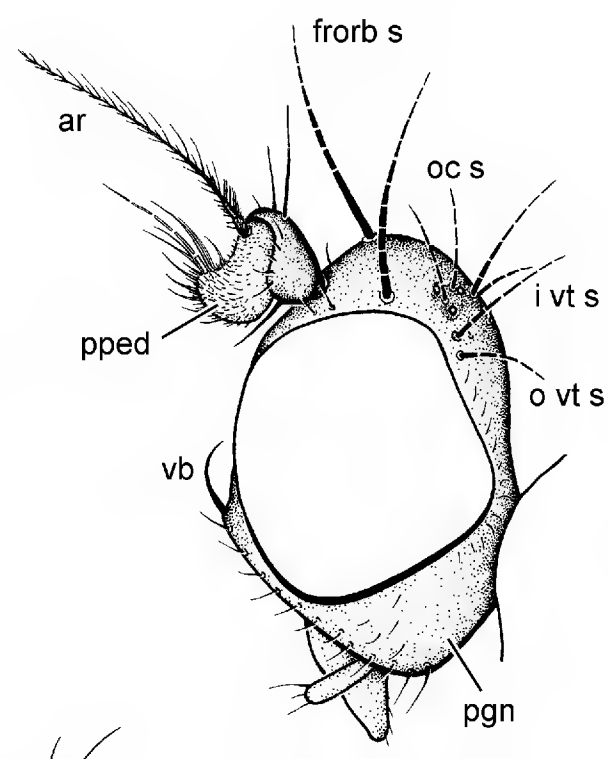
Larval first- and second-instars known only for Nearctic genus *Quametopia* Roháček & Barber (Roháček & Barber 2011). First-instar larva small (length: 0.9–1.5 mm), respiratory system metapneustic (Fig. 52); cephaloskeleton pale, weakly sclerotised (Fig. 53), with unpaired medial mouthhooks (Figs 54, 55), reduced cirri and posterior spiracle with 2 spiracular openings, but lacking spiracular peritreme (Fig. 57); second-instar larva resembling third-instar larva, with amphipneustic respiratory system and similar cephaloskeleton (including paired mouthhooks), but prothoracic spiracle simplified, clavate, with single spiracular opening (Fig. 59) and posterior spiracle with 2 spiracular openings (resembling first-instar larva) and spiracular peritreme well-developed (Fig. 58); third-instar larva (Fig. 56) slender, elongate (length: 3–5 mm), sub-cylindrical in shape, with distinct body segmentation; integument smooth, except for transverse rows of tiny spicules on dorsal and ventral surfaces, at least of abdominal segments; pseudocephalon (Figs 64, 65), with anteroventromedial emargination separating cephalic lobes, each with ventral cirri, composed of cuticular thornlets, atrium between them and each lobe bearing 2-segmented antenna dorsally; prothorax with small retractile prothoracic spiracles sub-laterally, each terminally palmate,



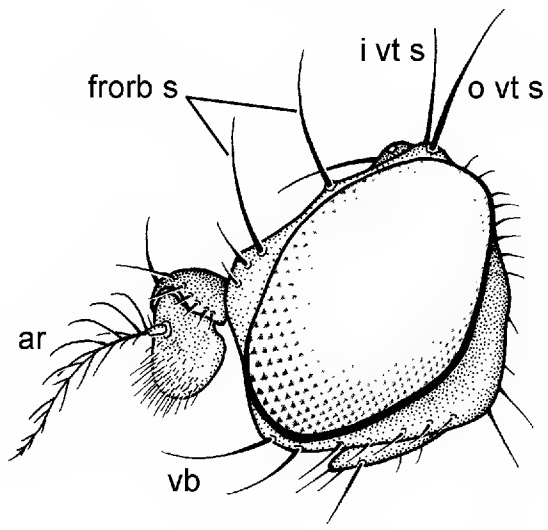
7 *Margdalops*



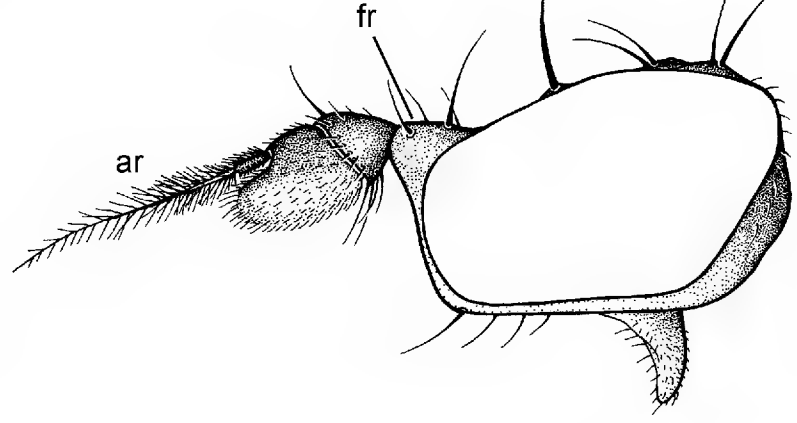
8 *Barbarista*



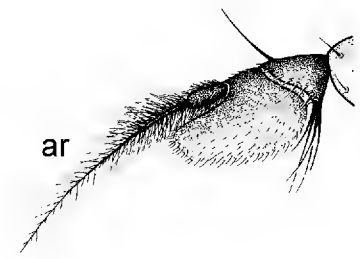
9 *Scelomyza*



10 *Amygdalops*



11 *Amnonthomyza*

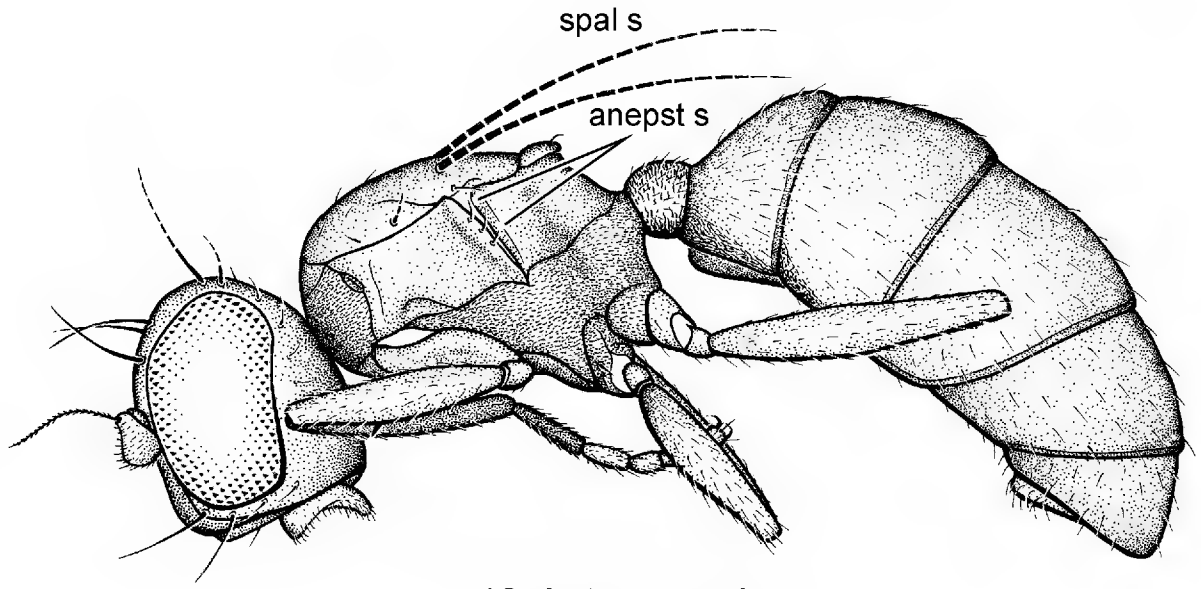


12 *Amnonthomyza*

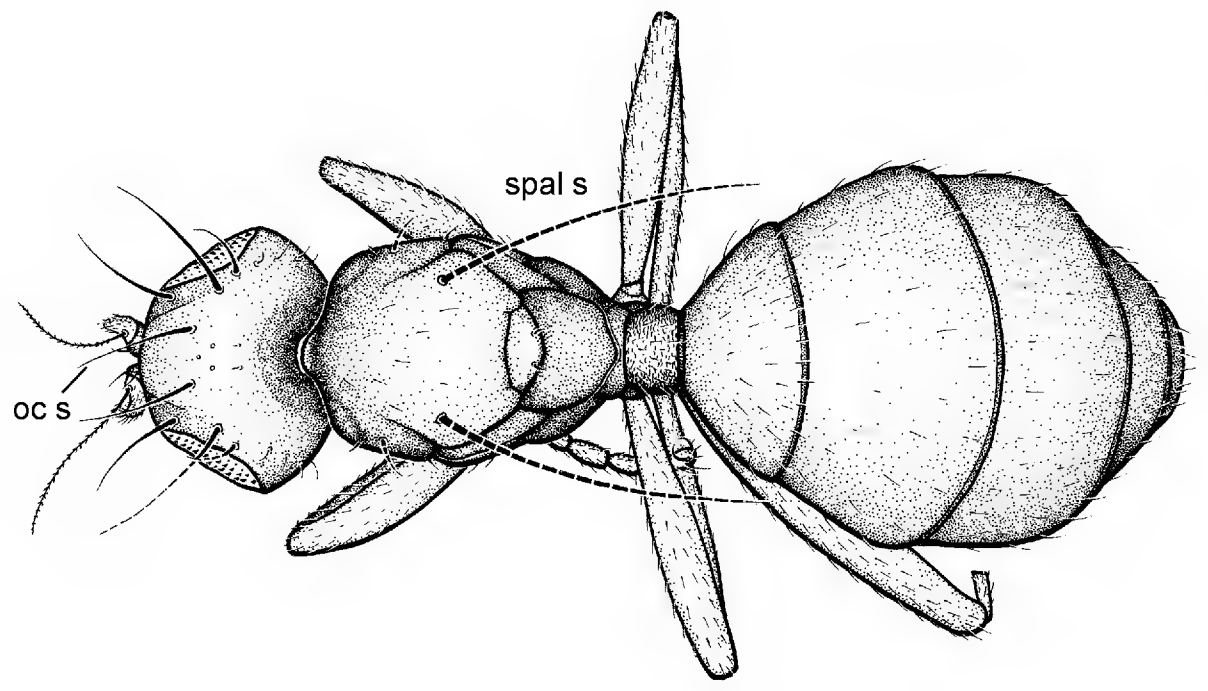
Figs 87.7–12. Heads and antenna of Anthomyzidae: (7) head of *Margdalops venustus* Roháček & Barraclough, lateral view; (8) same, *Barbarista guttata* Roháček, dorsolateral view; (9) same, *Scelomyza hirticornis* Séguy, lateral view (chaetotaxy reconstructed); (10) same, *Amygdalops thomasseti* Lamb; (11) same, *Amnonthomyza deplanata* Roháček; (12) antenna of *Amn. regina* Roháček, lateral view. Fig. 7 (Roháček & Barraclough 2003, fig. 48), Fig. 8 (Roháček 1993, fig. 1), Fig. 9 (Roháček 2014*a*, fig. 5), Fig. 10 (Roháček & Freidberg 1993, fig. 83), Figs 11, 12 (Roháček 1993, figs 79, 67, respectively).

Abbreviations: ar – arista; fr – frons; frorb s – fronto-orbital seta; i vt s – inner vertical seta; o vt s – outer vertical seta; oc s – ocellar seta; pgn – postgena; pped – postpedicel; sbvb s – subvibrissal seta; vb – vibrissa.

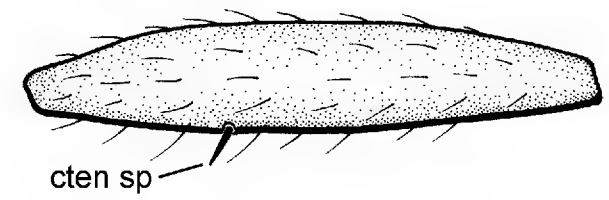
with 3–6 digitiform papillae (Fig. 62); cephaloskeleton (Figs 60, 61) of saprophagous type, relatively slender; mouthhooks paired, slender, sickle-shaped, with small ventral tooth; paired dental sclerites below mouthhooks small; intermediate sclerite relatively slender, separate from basal sclerite, H-shaped in ventral view, with narrow to broad cross-bridge; epistomal sclerite (Figs 60, 61) weakly sclerotised, pale, with 2–4 small perforations; basal sclerite with slender, anteriorly projecting parastomal bars, narrow, darker dorsal cornu and larger, but usually paler ventral cornu; dorsal cornu anterodorsally connected by simple (non-perforated) dorsal bridge; ventral cornu usually with small dorsal apodeme and ventrally connected by weakly sclerotised cibarium, with fine longitudinal ridges (Fig. 61); terminal abdominal segment sometimes with bulges in front of posterior spiracles and/or anal area; posterior spiracles (Fig. 63) on short, widely spaced, stump-like (often appearing



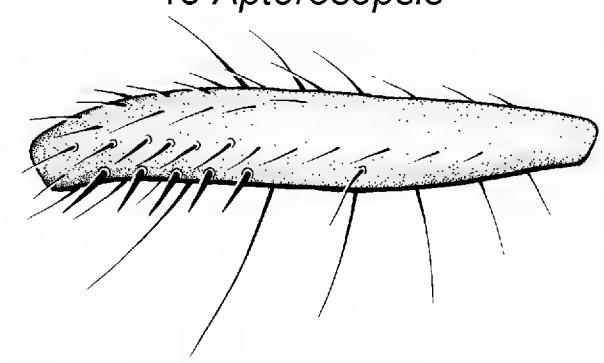
13 *Apterosepsis*



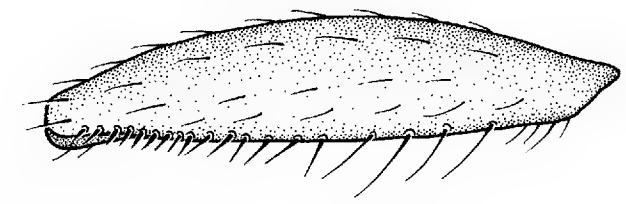
14 *Apterosepsis*



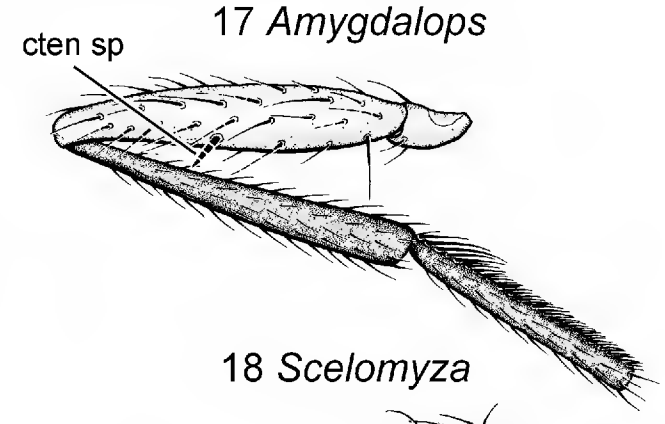
15 *Apterosepsis*



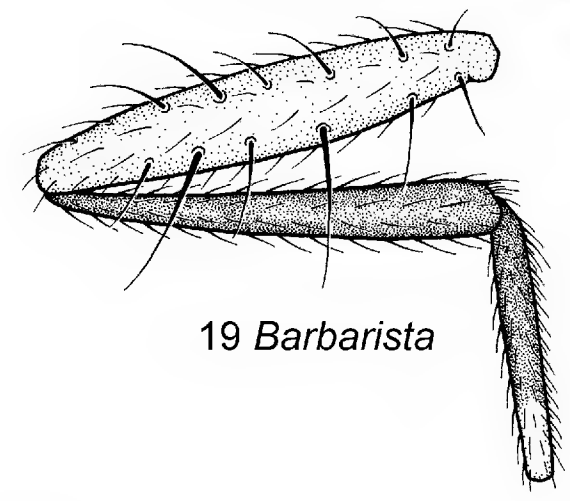
16 *Barbarista*



17 *Amygdalops*



18 *Scelomyza*



19 *Barbarista*

Figs 87.13–19. Habitus and legs of Anthomyzidae: (13) habitus of *Apterosepsis basilewskyi* Richards, lateral view (chaetotaxy reconstructed); (14) same, dorsal view (chaetotaxy reconstructed); (15) same, fore femur, posterior view; (16) same, *Barbarista guttata* Roháček, anterior view; (17) hind femur of *Amygdalops thomasseti* Lamb, posterior view; (18) fore trochanter, femur, tibia and tarsomere 1 of *Scelomyza hirticornis* Séguy, posterior view (chaetotaxy reconstructed); (19) fore femur, tibia and tarsomere 1 of *B. guttata* Roháček, posterior view. Figs 13–15 (Roháček 1998, figs 23–25), Fig. 17 (Roháček & Freidberg 1993, fig. 68), Fig. 18 (Roháček 2014*a*, fig. 7), Fig. 19 (Roháček 1993, fig. 10).

Abbreviations: anepst s – anepisternal seta; cten sp – ctenidial spine; oc s – ocellar seta; spal s – supra-alar seta.

2-segmented) processes; spiracular plate surrounded by spiracular peritreme, perforated by 3 oval spiracular openings in radial pattern, bearing 4 groups of finely branched peristigmatic tufts. For described larvae see de Meijere (1944), Nye (1958), Roháček (1992, 2009), Roháček & Barber (2011), Roháček & Freidberg (1993), Rotheray *et al*. (2014) and Séguy (1934).

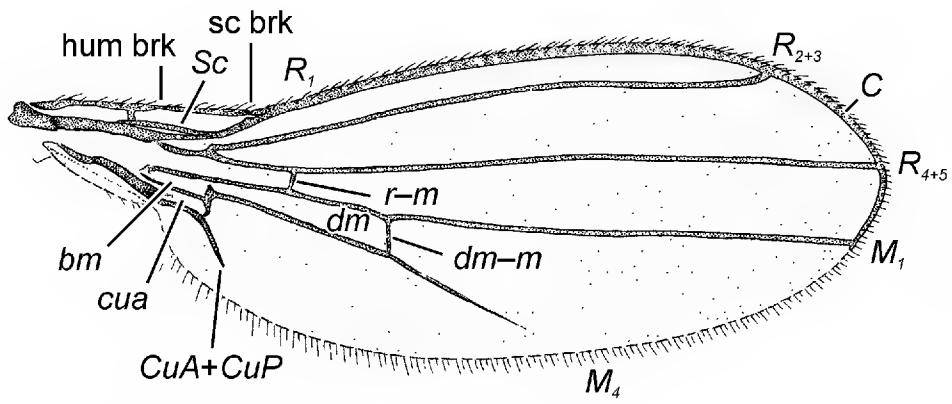
Puparium (Figs 70–74) elongate (length: 2.2–3.3 mm), barrel-shaped, more tapered anteriorly, less tapered to rounded posteriorly, usually convex, but sometimes (in non-Afrotropical *Typhamyza* Roháček), strikingly dorsoventrally flattened; integument of (empty) puparium yellow to brown in colour, densely, finely transversely wrinkled and ribbed; larval segmentation more or less visible; first visible (prothoracic) segment with (shortened) prothoracic spiracle (Fig. 70), dorsal surface strongly ribbed, with smooth, shallow suboval depression laterally, ventrally (Fig. 73) with blackish, palmately branched ornamentation; posterior end dorsally convex, densely wrinkled or ribbed, ventrally (Fig. 74), with anus surrounded by concentric wrinkles, ribs or other excrescences, posteriorly with stump-like spiracular processes (Figs 68, 69). For described puparia see Roháček (1992, 2009), Roháček & Barber (2011), Roháček & Freidberg (1993) and Rotheray *et al*. (2014).

Adult Anthomyzidae are superficially similar to those of some families of Opomyzoidea, particularly Opomyzidae (see Chapter 84), which also has larvae that develop in graminoid plants. They differ from species of the latter family in having the postvertical setae convergent, the anepimeron bare and the fore femur often with a ctenidial spine (secondarily lost in some genera). Other superficially similar families include the Asteiidae (see Chapter 92), Aulacigastridae (see Chapter 88), Periscelididae (subfamily Stenomicrinae) (see Chapter 91) and non-Afrotropical Teratomyzidae, but representatives of all these families differ markedly from Anthomyzidae in cephalic and thoracic setation and/or wing venation. Anthomyzidae are best distinguished from all other acalyptrate families by the structure of the internal male terminalia (see above).

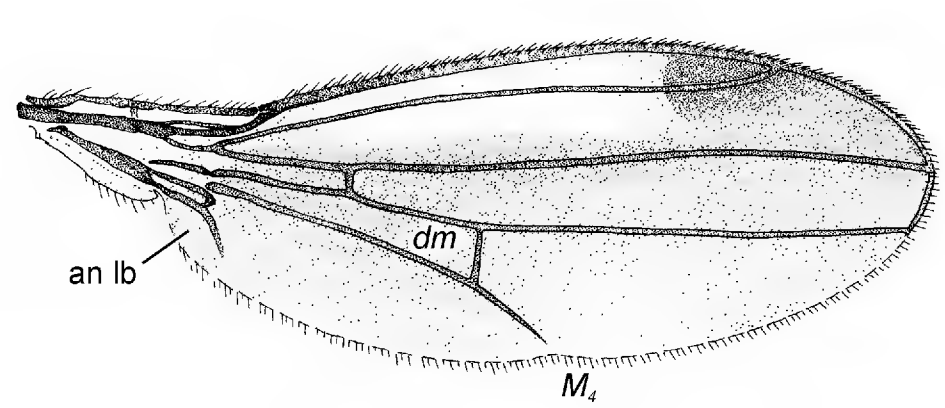
Biology and immature stages

The biology and immature stages of Anthomyzidae have hitherto only been studied in detail for some Palaearctic (see Roháček 2006, 2009 for review) and Nearctic species (Roháček & Barber 2005, 2011). In tropical regions, including the Afrotropics, immature stages and biology remain virtually unknown. Generally, the majority of species of Anthomyzidae are preferentially associated either with open damp habitats, such as marshland, grassland or in littoral zones, or with humid woodland undergrowth, especially in moist and/or waterlogged leafy or mixed forests.

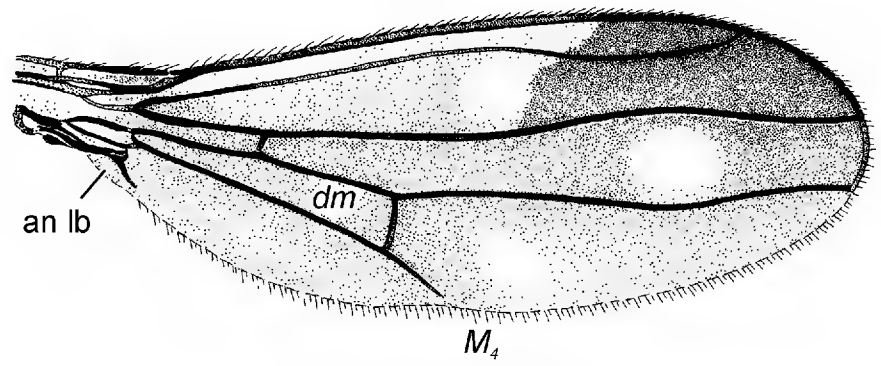
Larvae of Anthomyzidae appear to be largely phyto-saprophagous and are associated with dead or partly decomposed plant tissues, mainly in damaged plants, or as secondary invaders following infestations by other organisms, *e.g.*, by primary phytophagous insects (Roháček 2009) and, therefore,



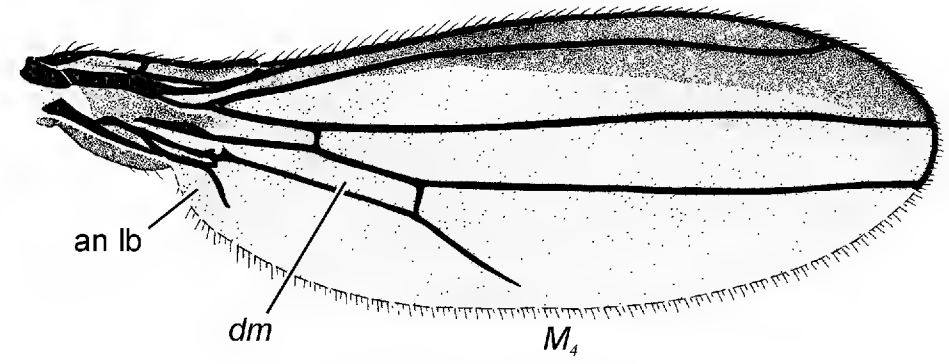
20 *Amydalops*



21 *Amygdalops*



22 *Amygdalops*



23 *Margdalops*

Figs 87.20–23. Wings of Anthomyzidae (dorsal views): (20) *Amygdalops trivittatus* Frey; (21) *A. thomasseti* Lamb; (22) *A. poecilus* Roháček; (23) *Margdalops venustus* Roháček & Barraclough. Figs 20–22 (Roháček 2004, figs 122, 123, 132), Fig. 23 (Roháček & Barraclough 2003, fig. 69).

Abbreviations: an lb – anal lobe; *bm* – basal medial cell; *C* – costal vein; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *dm* – discal medial cell; *dm–m* – discal medial crossvein; hum brk – humeral break; M_1 – first branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Sc* – subcostal vein; sc brk – subcostal break.

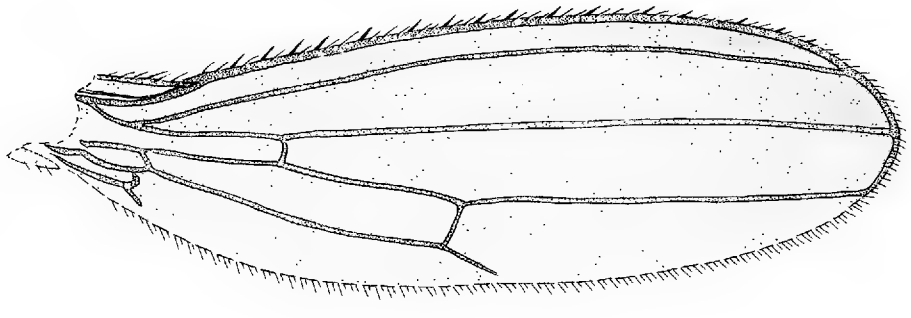
cause minimal damage to healthy plants (Roháček 1992, 2009). In reality, larvae are micro-saprophagous grazers on rotting host-plant tissues and micro-organisms involved in their decay, as demonstrated by the structure of their cephaloskeleton (Figs 60, 61). The same may be true for the mycophagous *Fungomyza albimana* (Meigen, 1830), as females have been observed ovipositing into partly decayed sporocarps (Roháček, unpubl.).

Larvae are known to develop chiefly between the damaged sheathing leaves of various graminoid plants, particularly grasses (Poaceae) and sedges (Cyperaceae), but also rushes (Juncaceae), reed-maces (Typhaceae) and allied families (Ferrar 1987: 78; Nye 1958, 1959; Roháček 1992, 1996, 2006, 2009, 2013*b*; Roháček & Barber 2005). Some are also able to develop in dead plants (e.g., the non-Afrotropical genera *Anagnota* Becker and *Typhamyza* – Roháček 1992, 2009), or as inquilines in galls of *Lipara* Meigen species (Chloropidae) and of the mite *Steneotarsonemus* Beer (Tarsonemidae) on Common reed (*Phragmites australis* (Cav.) Trin. ex Steud.) (some non-Afrotropical species of *Anthomyza* Fallén – Andersson 1976; Roháček 2009). Other species have been found to mine in damaged dicotyledonous plants, particularly beneath the epidermis of rotting stems or leaves (the non-Afrotropical genera *Paranthomyza* Czerny – de Meijere 1944; Hering 1943; Rotheray *et al*. 2014 and *Quametopia* – Roháček & Barber 2011) and possibly also in inflorescences (Barber & Roháček 2010: 1074). Some species may develop in ferns (Polypodiopsida) (a few non-Afrotropical *Arganthomyza* Roháček species – Roháček & Barber 2013), while others are known from horsetails (Equisetopsida) (two Nearctic species of *Anthomyza* – Roháček & Barber 2016). In addition, there are a few species associated with macrofungi. The European *Fungomyza albimana* has been reared from sporocarps of various fungi (Chandler 1978: 210, 2010: 438; Dely-Draskovits 1972) and the remaining two species of this genus are presumed to have similar biologies (Roháček 2009; Roháček & Barber 2004). *Reliquantha variipes* Roháček, 2013, from Great Britain, may also be trophically associated with tree fungi (Roháček 2013*c*) although there is a rearing record from rotten wood of sycamore in England (Smith 2017).

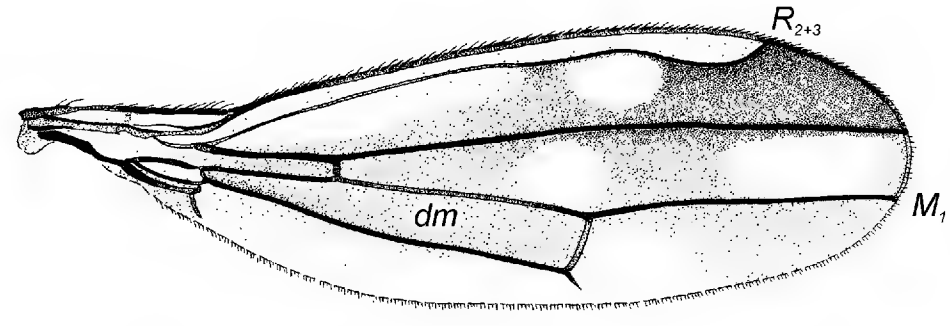
As regards the Afrotropical fauna, some biological information regarding host-plant associations for *Amygdalops thomasseti* Lamb, 1914, were provided by Roháček (2009, 2013*b*) and Roháček & Freidberg (1993), albeit based on collecting records from the southern Palaearctic. Anthomyzidae species may be univoltine, particularly at higher latitudes and elevations with cold climates, bivoltine or multivoltine and most species occurring in subtropical and tropical zones apparently have several generations per year. Adult Anthomyzidae are largely diurnal, usually with decreased activity in the hottest and driest periods of day in warm areas, but some are also nocturnal, as they have been repeatedly collected at light or in light traps, particularly in the tropics (Barber & Roháček 2010: 1074; Roháček 2004, 2009; Roháček & Barber 2005; Roháček & Barraclough 2003).

Economic significance

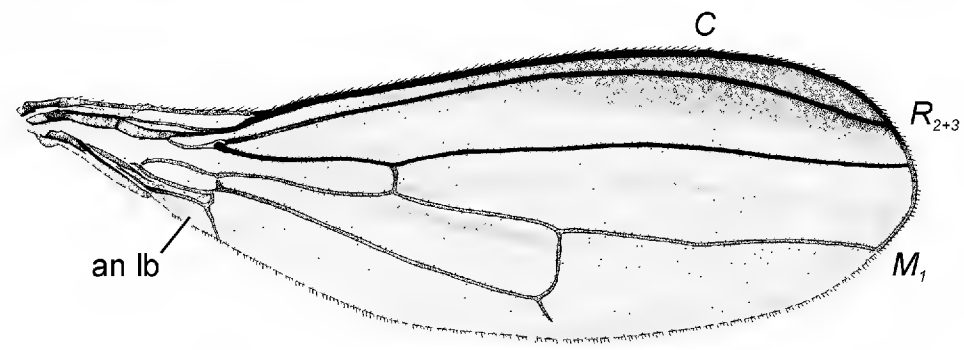
Although the Anthomyzidae are often abundant, particularly in marshes and other humid grassland habitats, they are of no economic importance, as they cause minimal damage to their host-plants. Their rare occurrence in cereal fields appears to be the result of secondary invasion following damage by other organisms (Roháček 2009).



24 *Scelomyza*



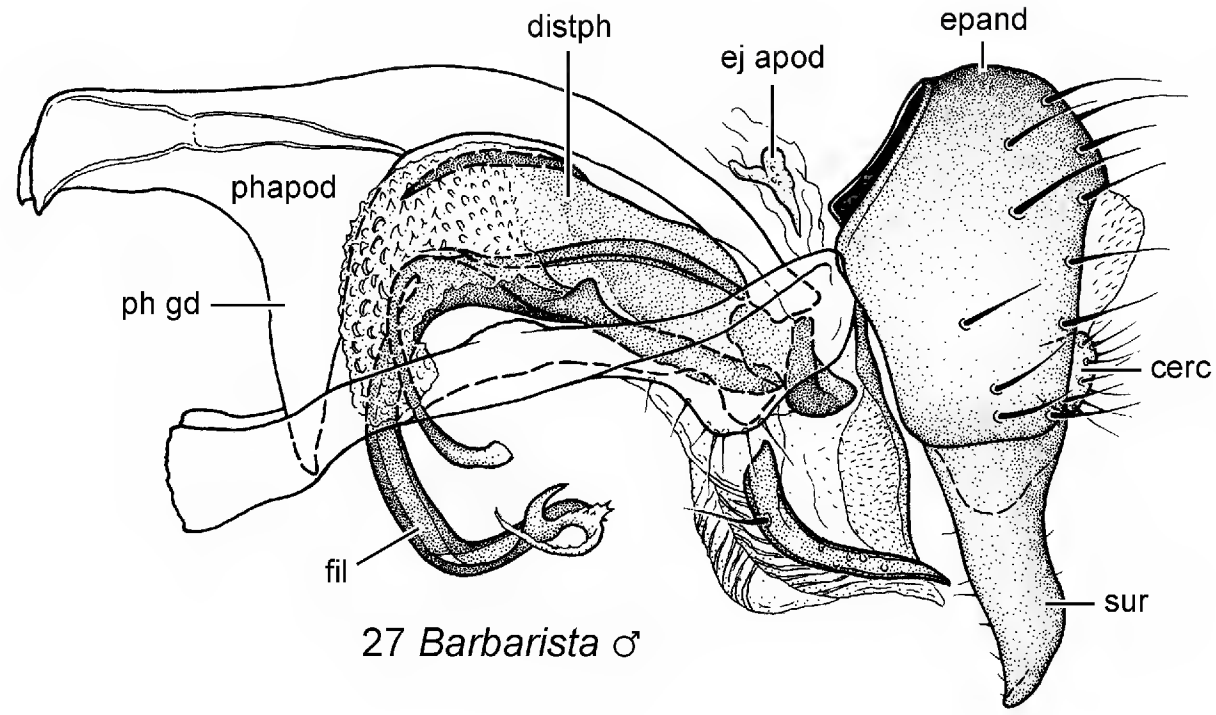
25 *Barbarista*



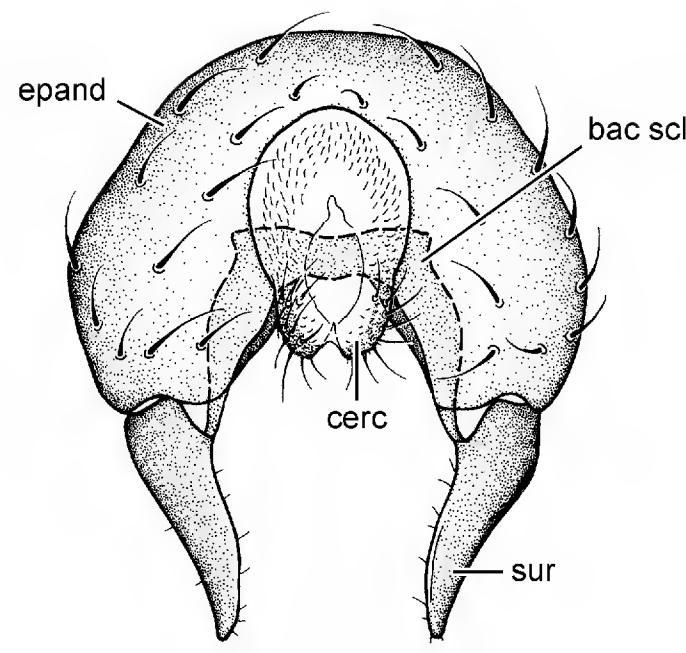
26 *Amnonthomyza*

Figs 87.24–26. Wings of Anthomyzidae (dorsal views): (24) *Scelomyza hirticornis* Séguy; (25) *Barbarista guttata* Roháček; (26) *Amnonthomyza regina* Roháček. Fig. 24 (Roháček 2014*a*, fig. 10), Figs 25, 26 (Roháček 1993, figs 54, 82).

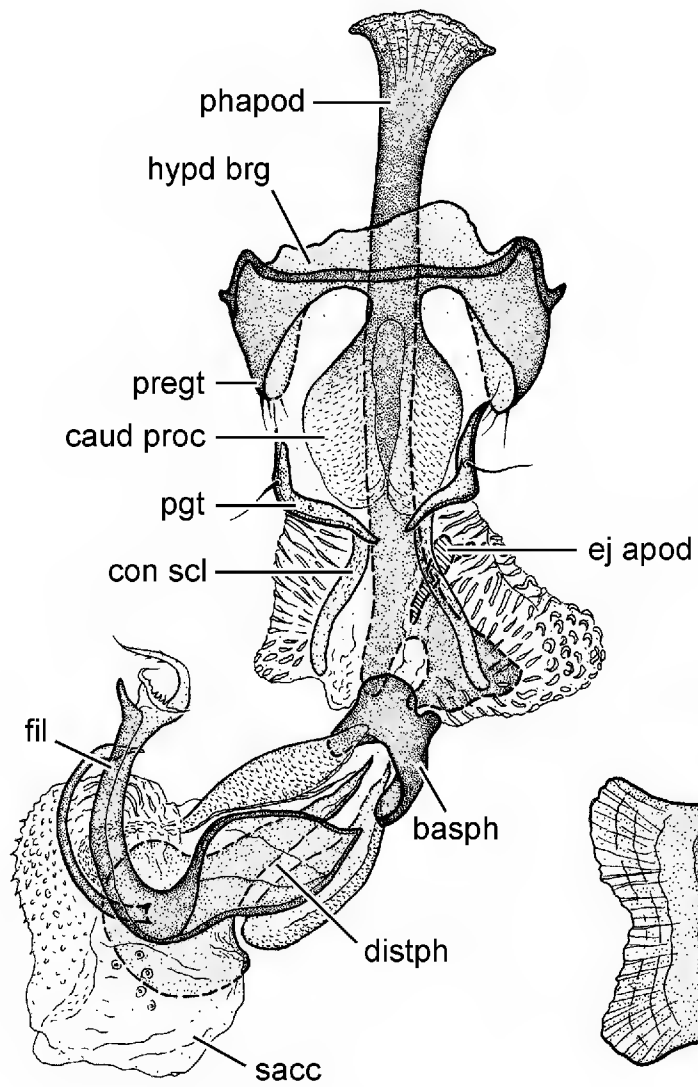
Abbreviations: an lb – anal lobe; *C* – costal vein; *dm* – discal medial cell; M_1 – first branch of media; R_{2+3} – second branch of radius.



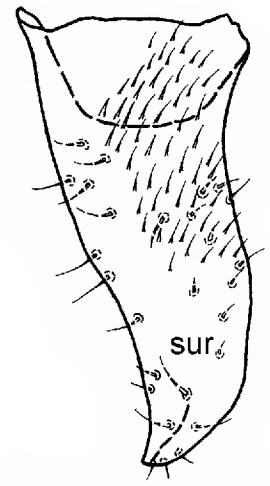
27 *Barbarista* ♂



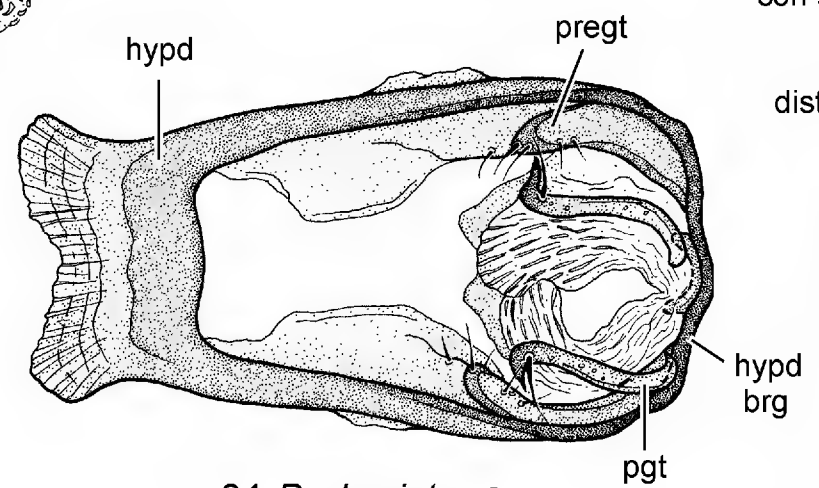
28 *Barbarista* ♂



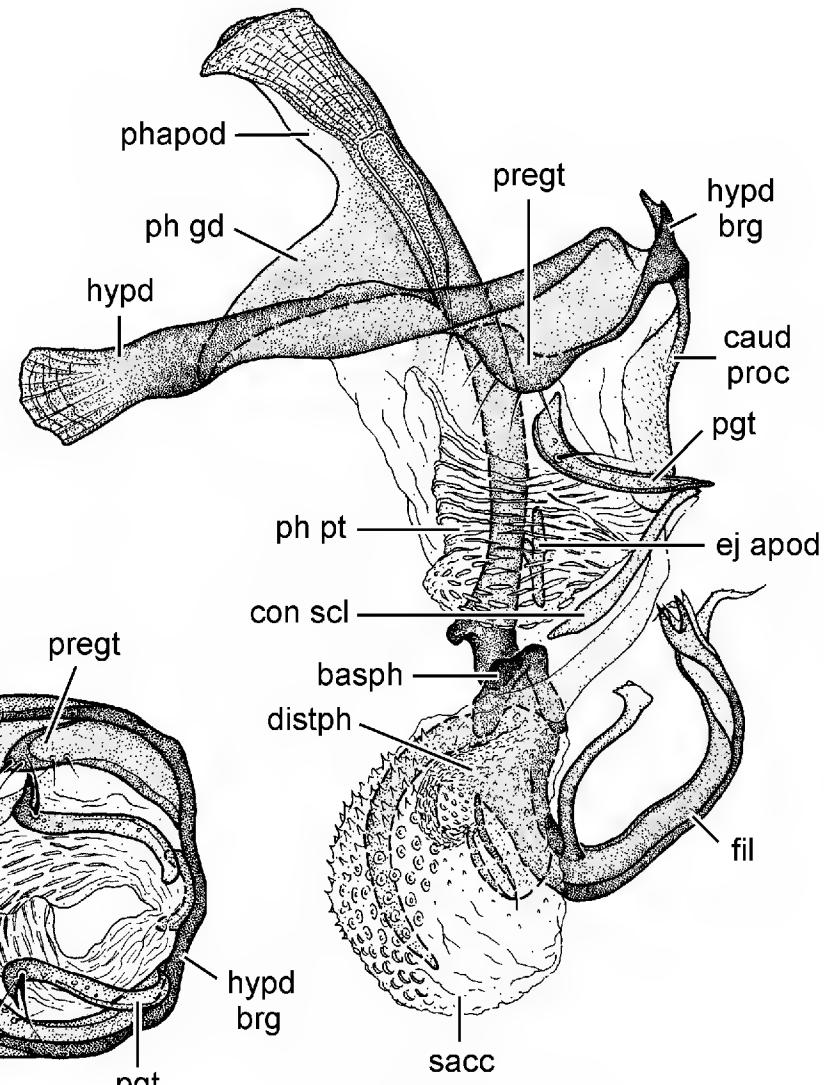
29 *Barbarista* ♂



30 *Barbarista* ♂



31 *Barbarista* ♂



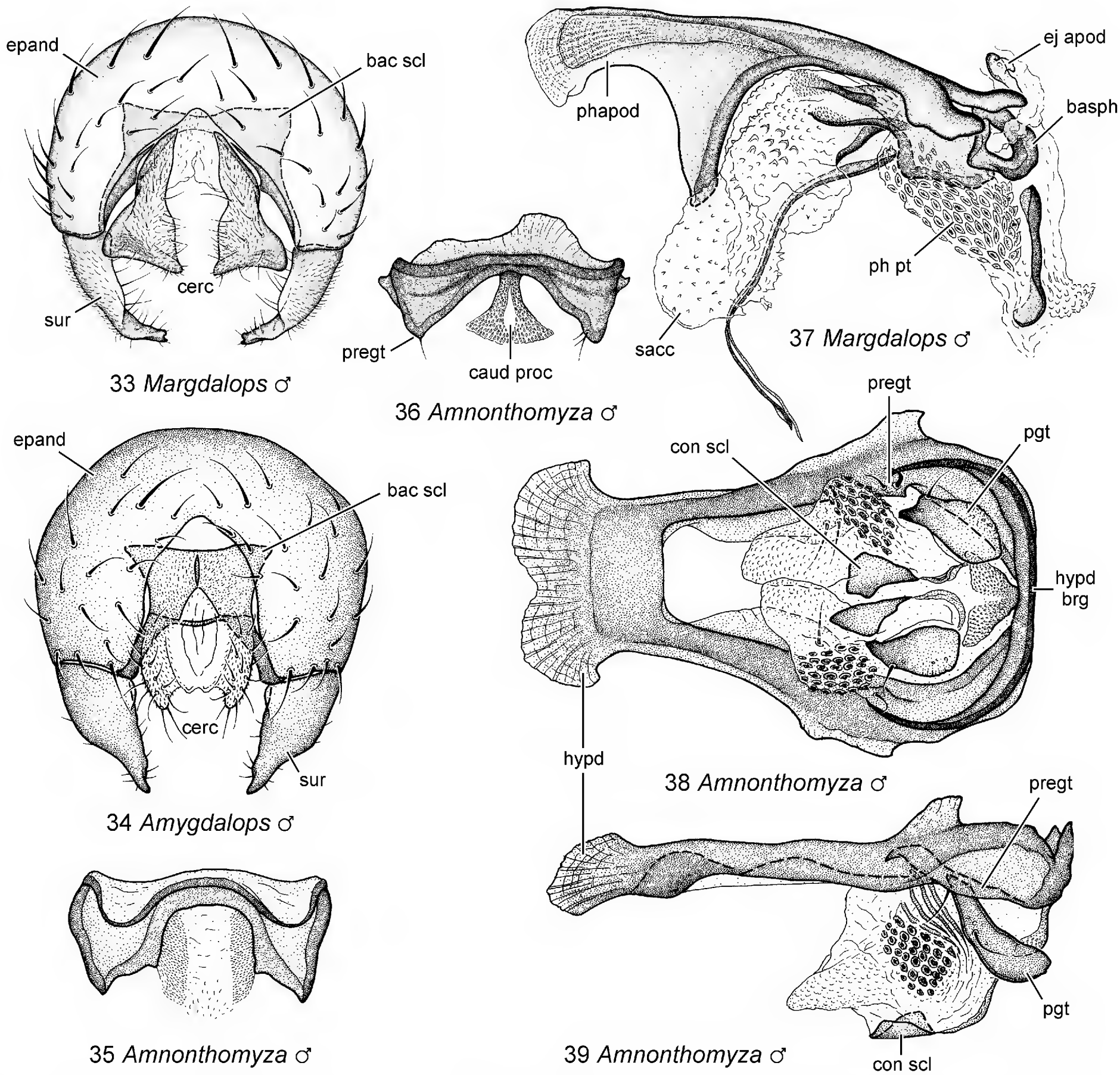
32 *Barbarista* ♂

Figs 87.27–32. Male terminalia of Anthomyzidae: (27) *Barbarista guttata* Roháček (terminalia in rest position), lateral view; (28) same, external terminalia, caudal view; (29) same, internal terminalia in erected position, caudal view; (30) same, surstylus, lateral view; (31) same, hypandrial complex, ventral view; (32) same, internal terminalia in erected position, lateral view. Figs 27–32 (Roháček 1993, figs 2–6, 11).

Abbreviations: bac scl – bacilliform sclerite; basph – basiphallus; caud proc – caudal process; cerc – cercus; con scl – connecting sclerite; distph – distiphallus; ej apod – ejaculatory apodeme; epand – epandrium; fil – filum; hypd – hypandrium; hypd brg – hypandrial bridge; pgt – postgonite; ph gd – phallic guide; ph pt – phallic part; phapod – phallapodeme; pregt – pregonite; sacc – saccus; sur – surstylus.

Classification

Anthomyzidae have long been considered as sister-group to the Opomyzidae (Hennig 1958; McAlpine 1989: 1460; Roháček 1998, 2006, 2013*a*). McAlpine (1989: 1460) placed these two families in the suprafamily Opomyzoinea, which, together with 11 other families form the suprafamilies Clusioinea, Agromyzoinea and Asteioinea, constituted the superfamily Opomyzoidea. Different classifications have been applied in the past however. Colless & McAlpine (1970: 729, 1991: 777), for example, assembled Anthomyzidae within the Asteioidea, while placing Opomyzidae in the Opomyzoidea. More

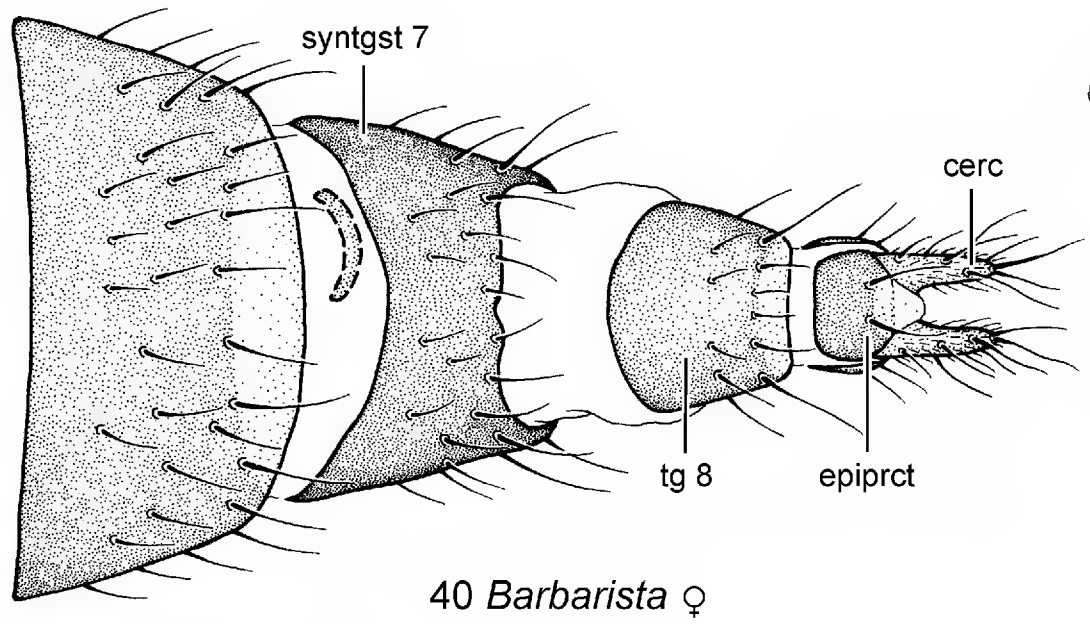


Figs 87.33–39. Male terminalia of Anthomyzidae: (33) external terminalia of *Margdalops venustus* Roháček, caudal view; (34) same, *Amygdalops thomasseti* Lamb; (35) hypandrial bridge of *Amnonthomyza deplanata* Roháček, caudal view; (36) same, *Amn. regina* Roháček; (37) phallic complex of *M. venustus*, lateral view; (38) hypandrial complex of *Amn. regina*, ventral view; (39) same, lateral view. Figs 33, 37 (Roháček & Barraclough 2003, figs 36, 39), Fig. 34 (Roháček & Freidberg 1993, fig. 67), Figs 35, 36, 38, 39 (Roháček 1993, figs 80, 66, 64, 65, respectively).

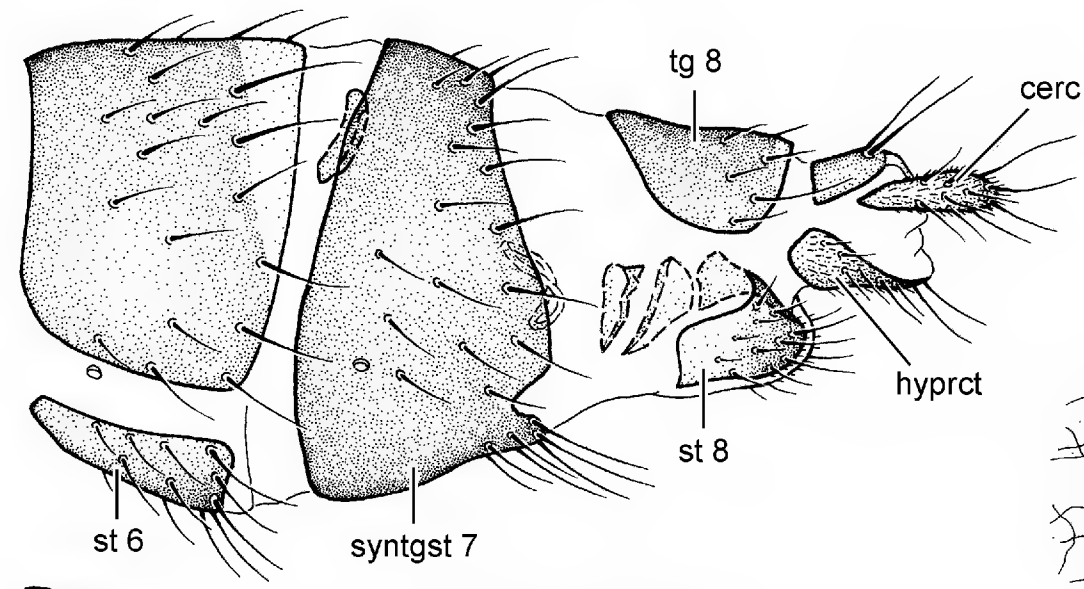
Abbreviations: bac scl – bacilliform sclerite; basph – basiphallus; caud proc – caudal process; cerc – cercus; con scl – connecting sclerite; ej apod – ejaculatory apodeme; epand – epandrium; hypd – hypandrium; hypd brg – hypandrial bridge; pgt – postgonite; ph pt – phallic part; phapod – phallapodeme; pregt – pregonite; sacc – saccus; sur – surstylus.

recently, in "phylogenetic" reconstructions using molecular data, the family Anthomyzidae has been clustered with quite different clades of acalyptrates, e.g., with Carnidae or Milichiidae + Chloropidae (Winkler *et al*. 2010) or with Heleomyzidae (Wiegmann *et al*. 2011). These sister-group relationships are weakly supported and in direct disagreement with morphological information and are, therefore, considered incorrect (Roháček 2013*a*). The Opomyzidae thus remains the most probable sister-group of the Anthomyzidae.

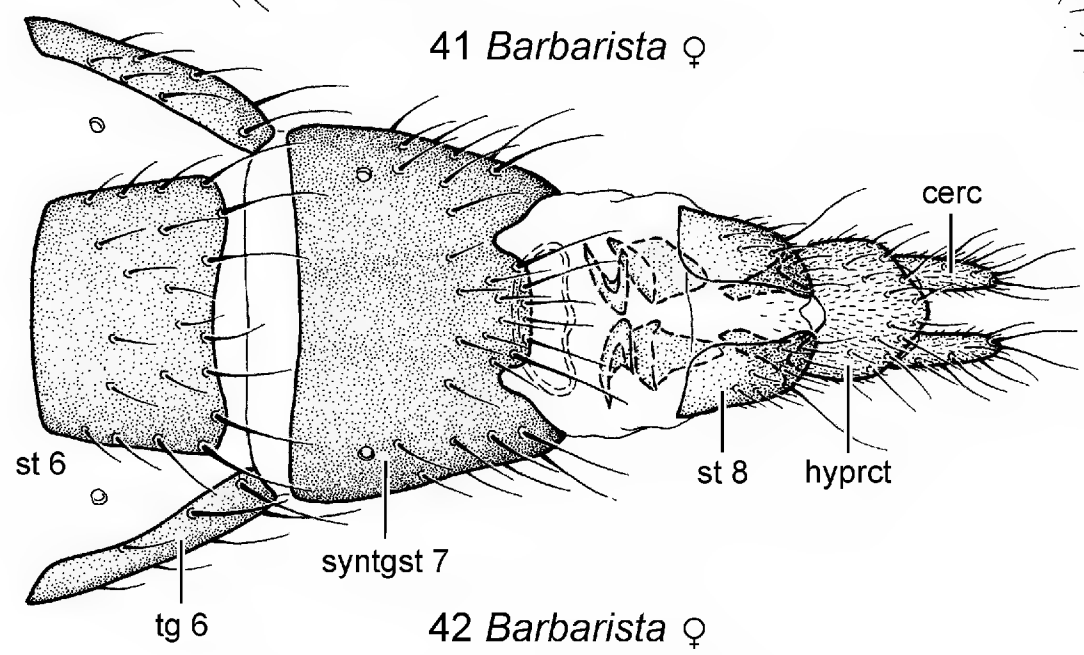
A total of 152 named species of Anthomyzidae, belonging to 28 genera are currently recognised (in 2018), including 12



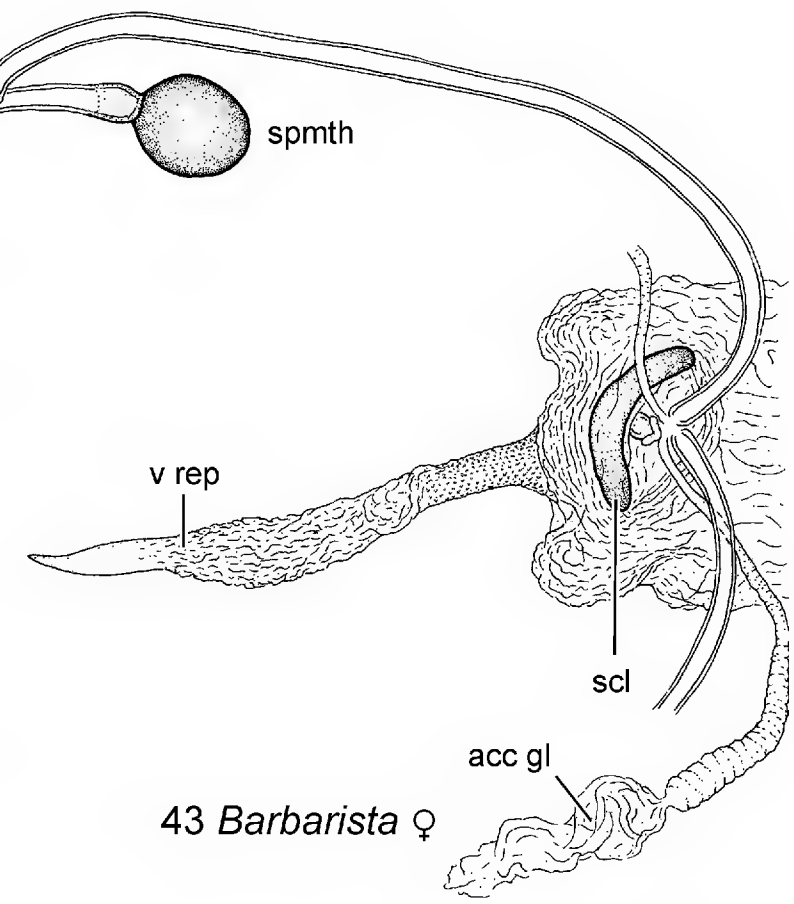
40 *Barbarista* ♀



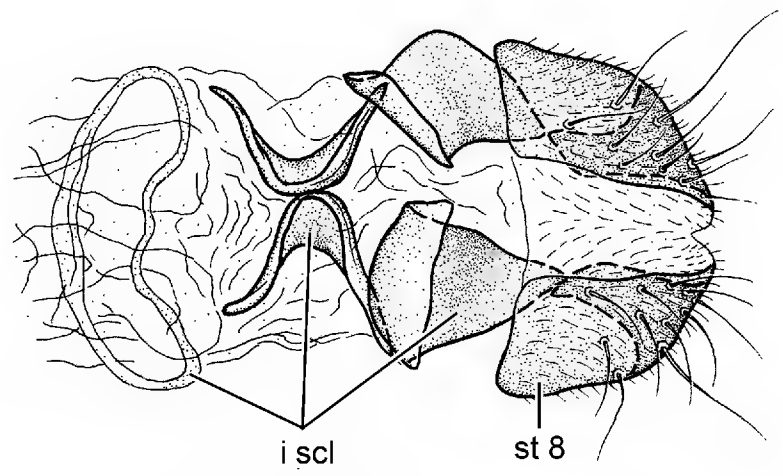
41 *Barbarista* ♀



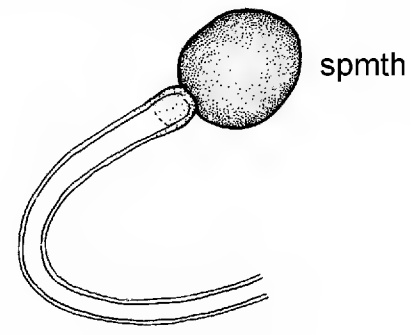
42 *Barbarista* ♀



43 *Barbarista* ♀



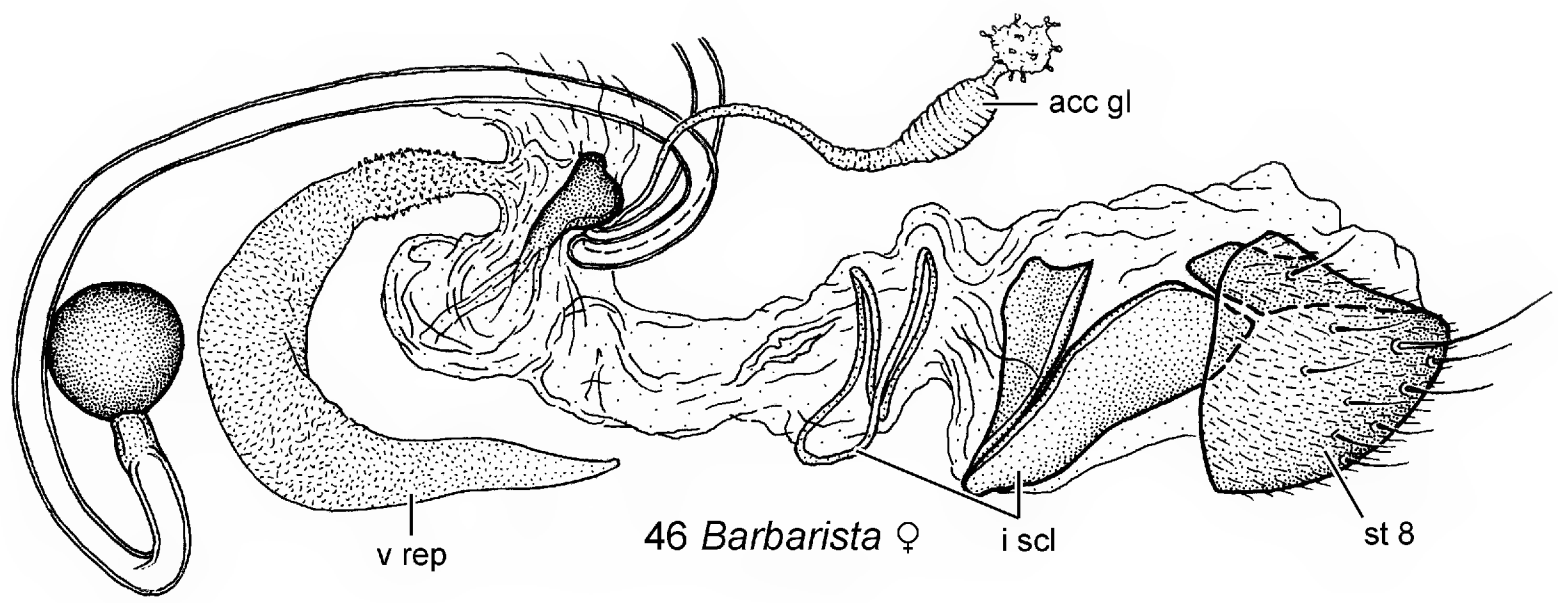
44 *Barbarista* ♀



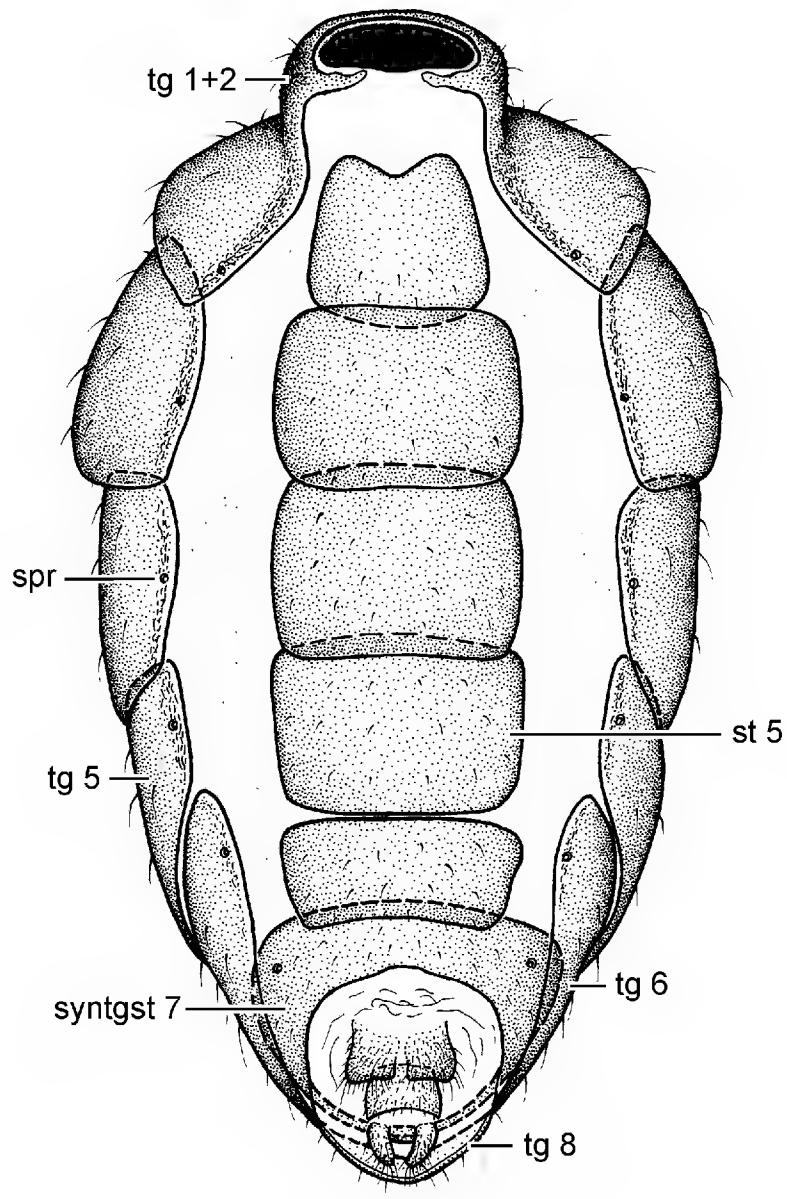
45 *Barbarista* ♀

Figs 87.40–45. Female abdomens and terminalia of Anthomyzidae: (40) postabdomen of *Barbarista guttata* Roháček, dorsal view; (41) same, lateral view; (42) same, ventral view; (43) same, distal part of female genital chamber, dorsal view; (44) same, proximal part of female genital chamber and sternite 8, ventral view; (45) same, spermatheca, lateral view. Figs 40–45 (Roháček 1993, figs 12–17).

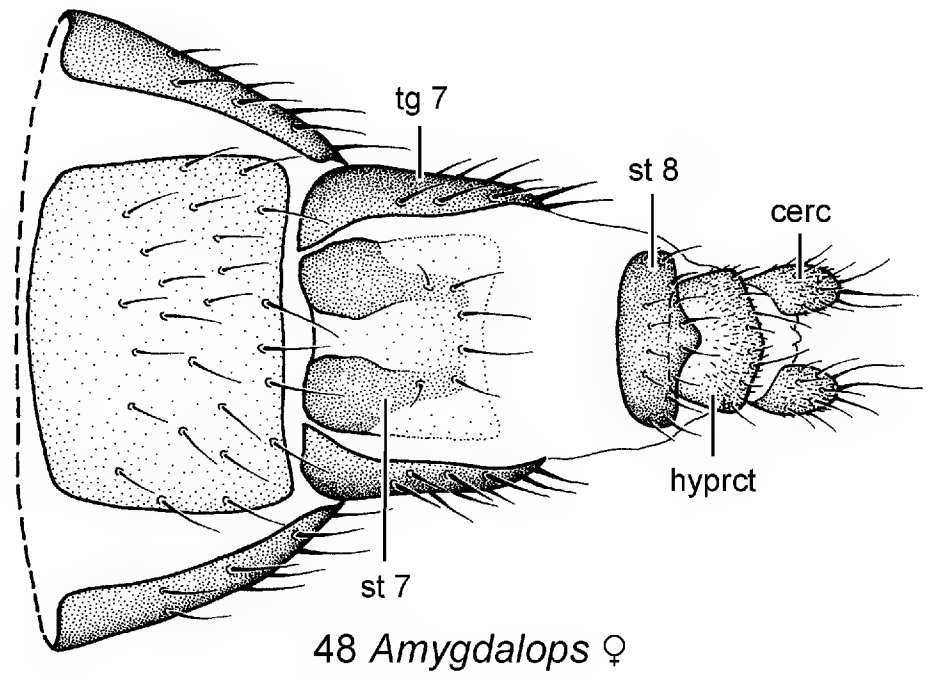
Abbreviations: acc gl – accessory gland; cerc – cercus; epiprct – epiproct; i scl – internal sclerites; hyprct – hypoproct; scl – sclerite; spmth – spermatheca; st – sternite; syntgst – syntergosternite; tg – tergite; v rep – ventral receptacle.



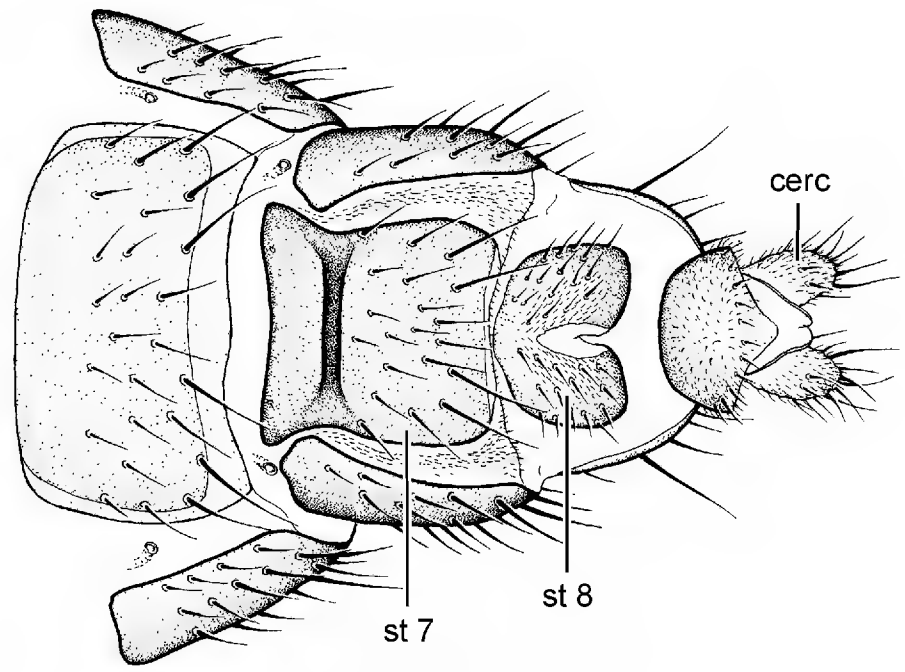
46 *Barbarista* ♀



47 *Apterosepsis* ♀



48 *Amygdalops* ♀



49 *Margdalops* ♀

Figs 87.46–49. Female abdomens and terminalia of Anthomyzidae: (46) female genital chamber and sternite 8 of *Barbarista brevifrons* Roháček, lateral view; (47) female abdomen of *Apterosepsis basilewskyi* Richards, ventral view; (48) female postabdomen of *Amygdalops thomasseti* Lamb, ventral view; (49) same, *Margdalops venustus* Roháček. Fig. 46 (Roháček 1993, fig. 35), Fig. 47 (Roháček 1998, fig. 47), Fig. 48 (Roháček & Freidberg 1993, fig. 77), Fig. 49 (Roháček & Barraclough 2003, fig. 49).

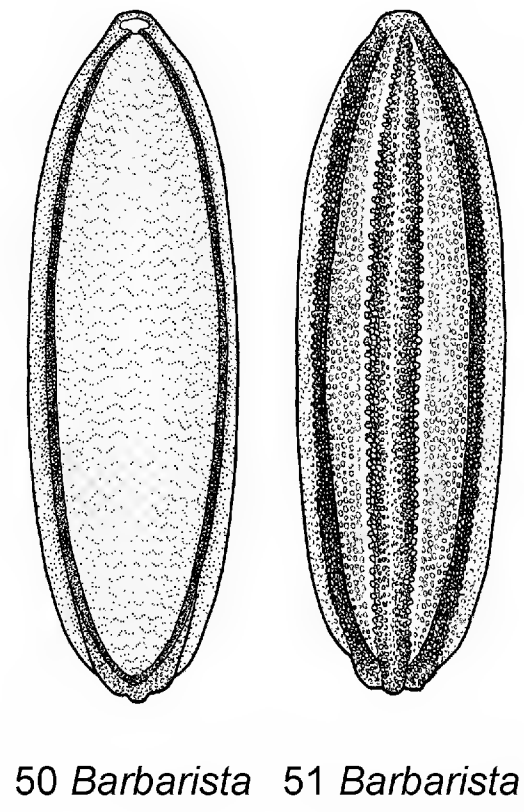
Abbreviations: acc gl – accessory gland; cerc – cercus; hyprct – hypoproct; i scl – internal sclerites; spr – spiracle; st – sternite; syntgst – syntergosternite; tg – tergite; v rep – ventral receptacle.

fossil species and three fossil genera (Roháček 2009, 2013*a*, 2014*a*, *b*, 2018; Roháček & Barber 2016). They are classified in two subfamilies: the fossil Protanthomyzinae, with the single genus *Protanthomyza* and 8 named species and Anthomyzinae, with two fossil and 25 extant genera and four fossil and 140 extant species. All described ancient Anthomyzidae are Tertiary, most originating from Baltic amber (Middle Eocene, 38–50 MY), *viz*. all *Protanthomyza* species, two species of *Lacrimyza* Roháček and one species of *Reliquantha* Roháček. Only one genus and species, *Grimalantha vulnerata* Roháček, 1998, is known from Dominican amber (Middle Miocene, 17–20 MY) (Roháček 1998, 2013*a*, 2014*b*). Thus, no fossil Anthomyzidae are currently known from the Afrotropical Region. The recent anthomyzid fauna of the Afrotropics consists of six genera and 26 named species (Roháček 2014*a*), but it is estimated, based on material available in collections, that there may be *ca* 90 species in more than 12 genera ultimately recognised. Consequently, the majority of available Afrotropical Anthomyzidae remain undescribed.

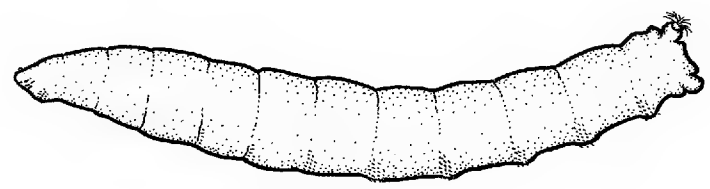
While the Holarctic fauna of Anthomyzidae is relatively well-known, due to monographic treatments by Roháček (2006, 2009), Roháček & Barber (2005, 2011, 2013, 2016) and supplementary studies by Roháček (2013*c*, 2018), all the tropical areas remain poorly investigated. The Neotropical fauna of Anthomyzidae is known only fragmentarily (Roháček 1998; Roháček & Barber 2005, 2009), although rich in species (Barber & Roháček 2010: 1074) and, similarly, in the Oriental Region only the genus *Amygdalops* Lamb has been studied in detail (Roháček 2008), while other groups of Anthomyzidae remain largely untouched in the region (Roháček 1987, 2018; Roháček & Barber 2013). In the Australasian and Oceanian Regions, the Anthomyzidae are obviously poorly represented, with a few species reported from New Zealand (Roháček 2007), Australia, Papua New Guinea and some Pacific islands (Roháček 2008). In this context, the Afrotropical Region has the fauna of Anthomyzidae slightly better studied; the single genus and species taxa were described from the region by Frey (1958), Lamb (1914, in Geomyzidae), Richards (1962, in Sepsidae) and Séguy (1938, in Opomyzidae); four additional speciose genera were treated by Roháček (1993, 2004) and Roháček & Barraclough (2003). Sabrosky (1980*a*: 650) also listed *Echidnocephalodes barbatus* (Lamb, 1914) among the Afrotropical Anthomyzidae, but this enigmatic genus and species was excluded from the family by Roháček (1998), as an acalyptrate of uncertain affinity, possibly related to Aulacigastridae or Periscelididae.

Identification

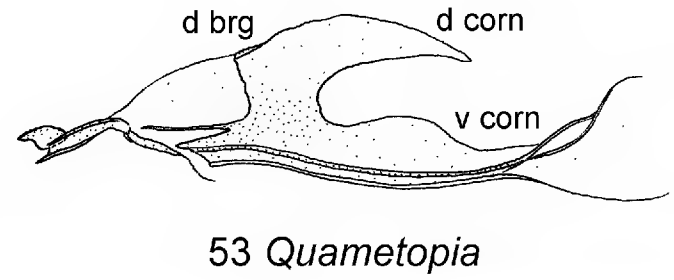
This review of the anthomyzid fauna of the Afrotropical Region only treats described genera. Unnamed taxa have, therefore, not been included in either the key or in the "Synopsis of the fauna" sections below. Anthomyzidae are normally micro-pinned in the field for later double-mounting (see Chapter 2).



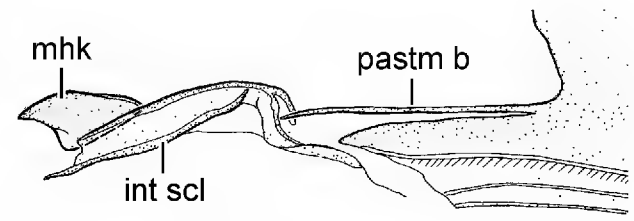
50 *Barbarista* 51 *Barbarista*



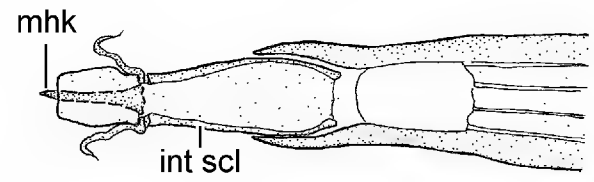
52 *Quametopia*



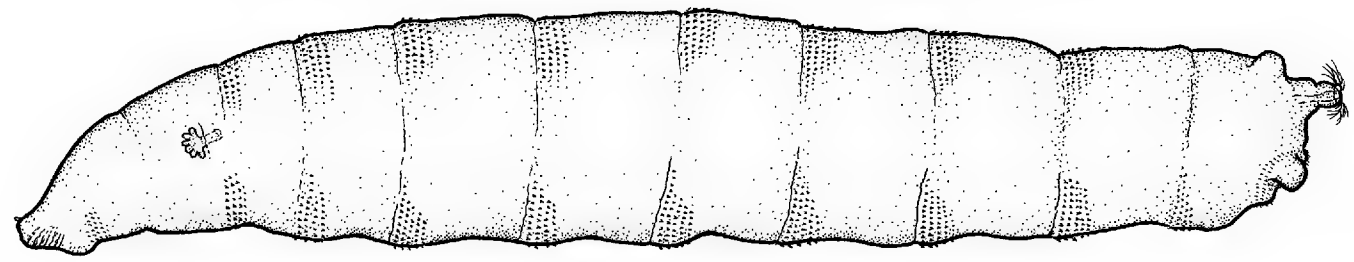
53 *Quametopia*



54 *Quametopia*



55 *Quametopia*



56 *Quametopia*

Figs 87.50–56. Immature stages of Anthomyzidae: (50) egg of *Barbarista guttata* Roháček, ventral view; (51) same, dorsal view; (52) habitus of first-instar larva of *Quametopia terminalis* (Loew), lateral view; (53) same, cephaloskeleton, lateral view; (54) same, anterior part of cephaloskeleton, lateral view; (55) same, ventral view; (56) same, third-instar larva, lateral view. Figs 50, 51 (Roháček 1993, figs 7, 8), Figs 52–56 (Roháček & Barber 2011, figs 46–49, 59).

Abbreviations: d brg – dorsal bridge; d corn – dorsal cornu; int scl – intermediate sclerite; mhk – mouthhook; pastm b – parastomal bar; v corn – ventral cornu.

Key to genera of Afrotropical Anthomyzidae

1. Wings and halteres absent (apterous); ant-mimicking minute flies (Figs 13, 14); thoracic chaetotaxy reduced (postpronotal, notopleural, presutural, postalar, scutellar and katepisternal setae minute or absent), but with extremely enlarged supra-alar seta (Figs 13, 14); abdomen basally with petiole, formed by constricted segment 1 and preabdominal tergites expanded ventrally; abdominal spiracles 2–6 inserted in tergal margins (Fig. 47) (male unknown). . . . . *Apterosepis* Richards

– Wings and halteres present (*e.g.*, Figs 1–3, 6); not ant-mimicking flies; thoracic chaetotaxy with most setae well-developed (*e.g.*, Figs 4, 5), supra-alar seta of normal size or small; abdomen never petiolate basally, preabdominal tergites smaller; abdominal spiracles 2–6 inserted in pleural membrane 2

2. Head distinctly higher than long, with ocellar triangle small, shifted posteriorly slightly behind vertex of head (Fig. 9); frons with 1 long fronto-orbital seta; antennal postpedicel with strikingly long pale setae on apex (Fig. 9); fore femur with distinct posteroventral ctenidial spine (Fig. 18) (male unknown). . . . . *Scelomyza* Séguy

– Head usually longer than high (rarely slightly higher than long), with ocellar triangle situated anterior to vertex of head (*e.g.*, Figs 4, 5, 8); frons with 2 long fronto-orbital setae; antennal postpedicel ciliate, without long setae (*e.g.*, Figs 7, 8, 10, 11); fore femur without ctenidial spine (*e.g.*, Fig. 19) 3

3. Antenna porrect (*e.g.*, Figs 8, 11, 12), with arista densely and long hirsute, particularly basally; base of wing strongly narrowed, due to reduced anal lobe (*e.g.*, Figs 25, 26); female tergite and sternite 7 fused (*e.g.*, Figs 40–42), forming complete annular syntergosternum 7; female sternite 8 longitudinally divided, with posterior bare parts recurved and invaginated into abdominal segment 8 (*e.g.*, Figs 41, 44) 4

– Antenna distinctly geniculate between pedicel and postpedicel (*e.g.*, Figs 7, 10), with arista sparsely ciliate to pectinate; base of wing wide, anal lobe distinctly developed (*e.g.*, Figs 20–23); female tergite and sternite 7 disparate (at most sternite 7 anteriorly partly fused to lateroventral corners of tergite 7) (*e.g.*, Figs 48, 49); female sternite 8 undivided, at most posteromedially incised (*e.g.*, Fig. 49), with posterior part never invaginated 5

4. Basal thickened segment of antennal arista elongate (Figs 11, 12); fore femur without thickened anteroventral setae; wing membrane brownish, with pale maculae absent or small (Fig. 26); vein R_{2+3} curved along costal vein (*C*); vein M_1 sinuate (Fig. 26); male terminalia with hypandrial bridge with small medial caudal process, split or bipartite (Figs 35, 36); postgonite robust (Figs 38, 39), heavily sclerotised; filum of distiphallus compact, without lateral branch; female genital chamber without sclerite at insertion of spermathecal ducts; ventral receptacle reduced, indistinct . . . . . *Amnonthomyza* Roháček

– Basal thickened segment of antennal arista short (Fig. 8); fore femur with short thickened anteroventral setae (Fig. 16); wing membrane (Fig. 25) dark brown with pale maculate pattern; vein R_{2+3} strongly sinuate; vein M_1 relatively straight (Fig. 25); male terminalia with hypandrial bridge with long, flat, medial caudal process (Figs 29, 32); postgonite slender (Figs 29, 32); filum of distiphallus with slender side branch in addition to main shaft (Figs 29, 32); female genital chamber with sickle-shaped sclerite at insertion of spermathecal ducts; ventral receptacle membranous, large, long and acutely pointed (Figs 43, 46). . . . . *Barbarista* Roháček

5. Antennal arista pectinate (Figs 4, 10); occiput without silvery fascia (Fig. 4); thorax with mesonotum with reduced presutural seta; anterior dorsocentral seta situated more posteriorly (Fig. 4); wing membrane unicolourous hyaline, pale, with subapical darkening or brown, with white maculae; discal medial cell (*dm*) usually long; distal part of vein M_4 short (Figs 1–3, 20–22); male terminalia with cerci small, weakly sclerotised (Fig. 34); bacilliform sclerite narrow, longer medially (Fig. 34); female terminalia with sternite 7 distinctly modified (Fig. 48). . . . . *Amygdalops* Lamb

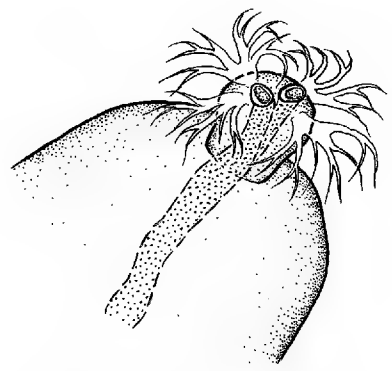
– Antennal arista ciliate (Fig. 7); occiput with pair of silvery micro-tomentose fascia (Fig. 5); thorax with mesonotum with well-developed presutural seta (Fig. 5); anterior dorsocentral seta situated more anteriorly (Fig. 5); wing membrane (Fig. 23) markedly darkened along anterior margin; discal medial cell (*dm*) short, very narrow; distal part of vein M_4 long (Fig. 23); male terminalia with cerci enlarged, heavily sclerotised (Fig. 33); bacilliform sclerite broad, medially shortened (Fig. 33); female terminalia with sternite 7 simple, plate-shaped, at most slightly modified (Fig. 49). . . . . *Margdalops* Roháček & Barraclough

Synopsis of the fauna

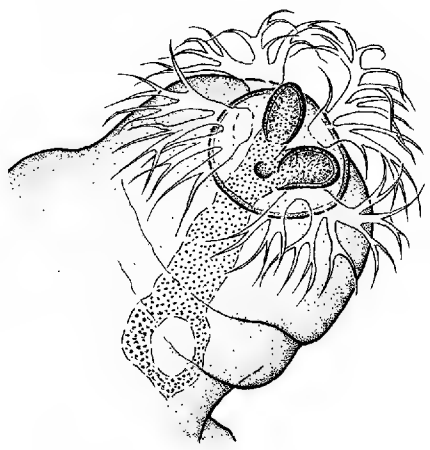
***Amnonthomyza* Roháček** (Anthomyzinae)**.** An endemic genus of two species confined to Madagascar (Roháček 1993), but additional species can be expected to occur there. Species of the genus are similar in general habitus to *Barbarista* species (refer to Fig. 6), in having distinctly porrect antennae, a densely hirsute antennal arista (Figs 11, 12), an elongated head, with the frons anteriorly projecting (Fig. 11) and a strongly reduced anal lobe of the wing (Fig. 26). The genus differs from *Barbarista*,

however, in the markedly elongate basal segment of the arista (Figs 11, 12), the short cephalic and thoracic setae, the single dorsocentral seta, wing vein R_{2+3} simply curved and vein M_1 sinuate (Fig. 26) and a number of peculiarities of the male terminalia (including the robust postgonite and plate-shaped connecting sclerite near base of phallus) (Figs 35, 36, 38, 39) and female terminalia (see key above). The type species, *A. regina* Roháček, 1993, is the largest known species of Anthomyzidae, with a maximum body length of 4.5 mm. Type material was collected from densely shaded shrubbery in very damp forest. No other biological information is available and immature stages of the species remain unknown. An identification key to the two named species was provided by Roháček (1993).

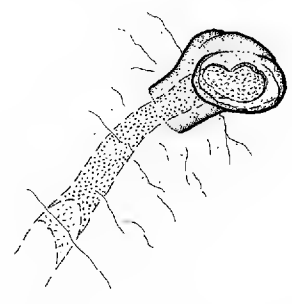
***Amygdalops* Lamb** (Anthomyzinae)**.** A genus of 24 described species occurring in the Afrotropical, Australasian/Oceanian, Oriental and Palaearctic Regions (Roháček 2004, 2008, 2009, 2018). Some additional species await description and other new species should be expected. The genus is well-represented in the Afrotropics, with 11 named and a number of unnamed species and is widespread, ranging from Cabo Verde, through tropical and subtropical belts of the continental Afrotropics, to Madagascar, Mauritius and Seychelles in the Indian Ocean (Roháček 2004). *Amygdalops* species are slender flies, with very convex oval eyes, a long-pectinate antennal arista (Fig. 10), a fore femur lacking a ctenidial spine and usually brown patterned wings, often with a distinctive subapical dark macula (Figs 21, 22). For additional characters refer to the diagnosis of Roháček (2004). *Amygdalops* species appear to be associated with usually tall grasses in various grassland habitats and lush vegetation at the margins of water bodies (Roháček 2004), as particularly demonstrated by *A. thomasseti*, the



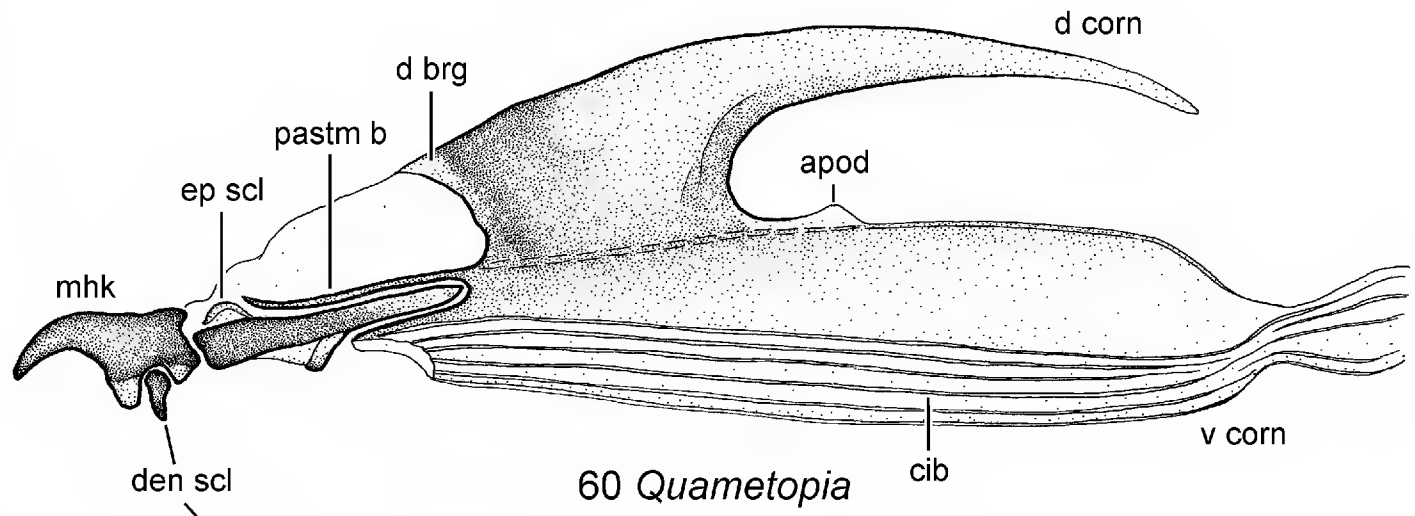
57 *Quametopia*



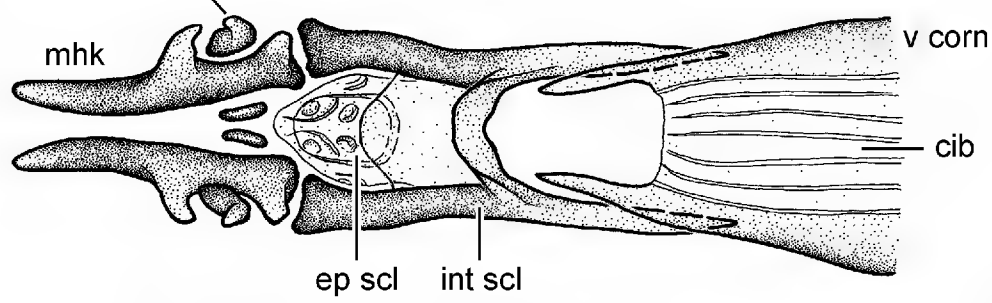
58 *Quametopia*



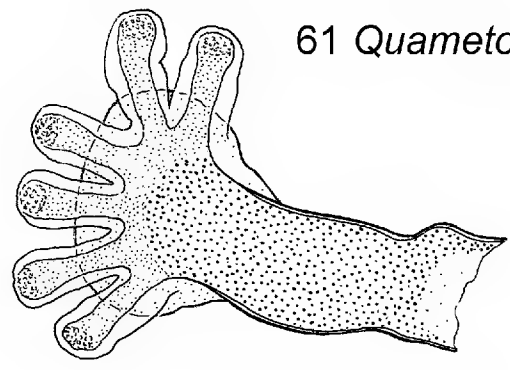
59 *Quametopia*



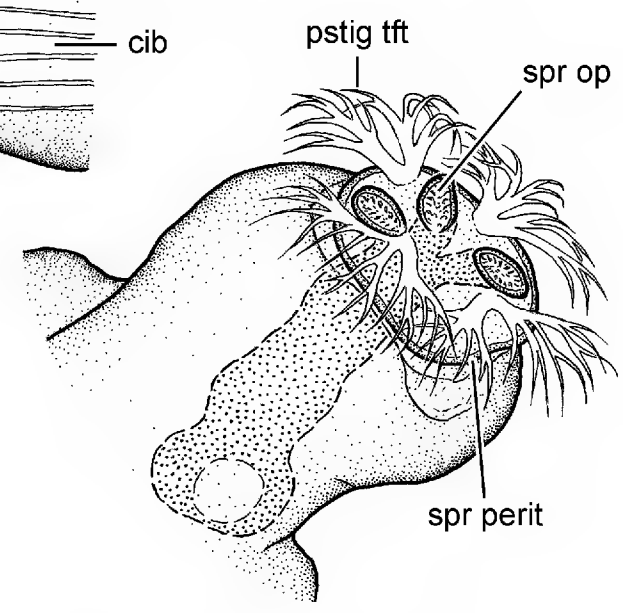
60 *Quametopia*



61 *Quametopia*



62 *Quametopia*



63 *Quametopia*

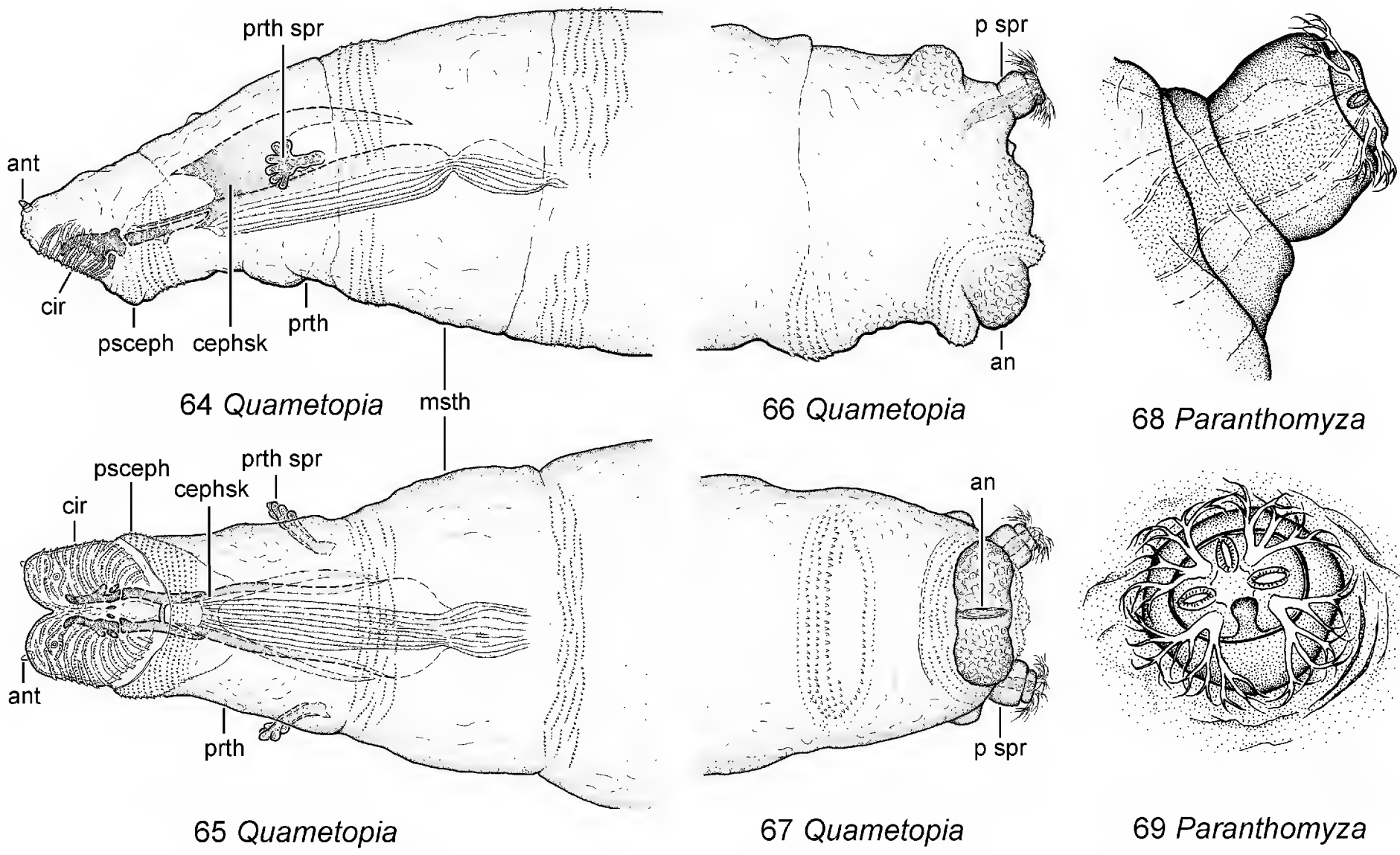
Figs 87.57–63. Immature stages of Anthomyzidae: (57) left posterior spiracle of *Quametopia terminalis* (Loew), first-instar larva, lateral view; (58) same, second-instar larva, dorsolateral view; (59) same, left prothoracic spiracle, widest extension, lateral view; (60) same, third-instar larva, cephaloskeleton, lateral view; (61) same, anterior part of cephaloskeleton, ventral view; (62) same, left prothoracic spiracle, sublateral view; (63) same, left posterior spiracle dorsolateral view. Figs 57–63 (Roháček & Barber 2011, figs 52, 57, 58, 60–63).

Abbreviations: apod – apodeme; cib – cibarium; d brg – dorsal bridge; d corn – dorsal cornu; den scl – dental sclerite; ep scl – epistomal sclerite; int scl – intermediate sclerite; mhk – mouthhook; pastm b – parastomal bar; pstig tft – peristigmatic tuft; spr op – spiracular opening; spr perit – spiracular peritreme; v corn – ventral cornu.

type species of the genus (Roháček 2009, 2013*b*; Roháček & Freidberg 1993). In the Afrotropics, adults of some species are probably active throughout the year. Of the 11 named species recorded from the region one, *A. nigrinotum* Sueyoshi & Roháček, 2003, is probably introduced into Seychelles from the Oriental Region. An identification key to species was provided by Roháček (2004).

***Apterosepsis* Richards** (Anthomyzinae)**.** A monotypic genus, with the single described species, *A. basilewskyi* Richards, 1962 (Figs 13, 14), a wingless ant-mimic from Tanzania. The species was originally described in the family Sepsidae (Richards 1962), but was later transferred to Anthomyzidae (McAlpine 1978, 1990) and to Chloropidae (Sabrosky 1980*b*: 697). More recently, Roháček (1998) definitively confirmed its affiliation with Anthomyzidae. Apart from its peculiar body shape, with the petiolate abdomen, the genus is distinguished by the ocellar setae situated off (in front of) the ocellar triangle (Fig. 14), reduction of the thoracic chaetotaxy, except for the enormously enlarged supra-alar setae (Figs 13, 14), the presence of minute anepisternal setulae (Fig. 13), presence of a ctenidial spine on the fore femur (Fig. 15) and spiracles 2–6 embedded in the margins of the female abdominal tergites (Fig. 47). *Apterosepsis basilewskyi* was re-described in detail by Roháček (1998) and is known only from two females collected in June at 2,750 m.

***Barbarista* Roháček** (Anthomyzinae)**.** An endemic genus of five described species, all from the continental Afrotropics, ranging from Nigeria to Kenya, south to Zimbabwe. Some additional species are expected to be discovered in the region. The genus can be recognised on the basis of the porrect antennae, the densely hirsute antennal arista, the more or less distinctly projecting frons (Fig. 8) and the white-maculate wings, with strongly narrowed base (Fig. 25). The genus differs from the similar *Amnonthomyza* in having the basal thick segment of the arista short (Fig. 8), 2 dorsocentral setae, the fore tibia and fore basitarsus (at least partly) blackish brown (Fig. 19), the fore femur with a row of short thick anteroventral setae (Fig. 16), wing vein R_{2+3} sinuate, but vein M_1 relatively straight, the cell *dm* long (Fig. 25) and the differently formed male (Figs 27–32) and female terminalia (Figs 40–45) (see Roháček 1993, for further detail). Nothing is currently known about habitat preferences, host-plant associations or immature stages. Adults have been collected in April to July and in November to January. An identification key to all named species was provided by Roháček (1993).

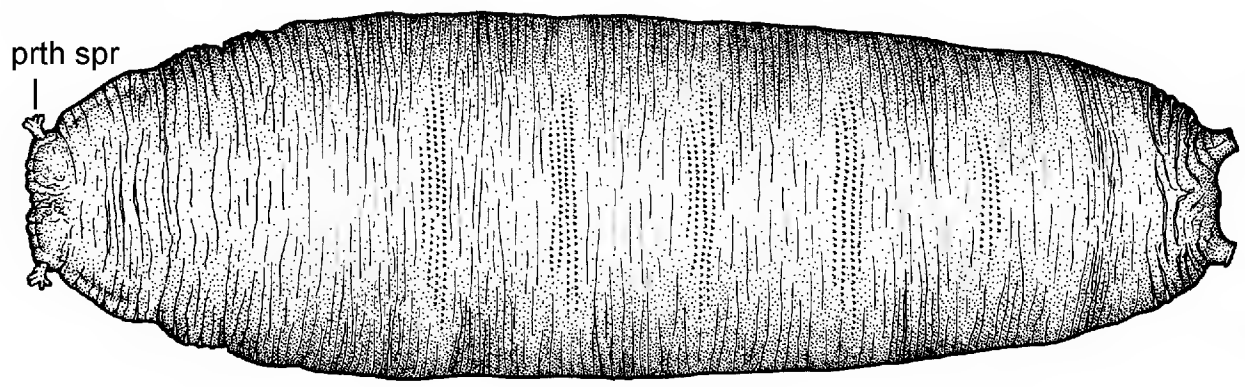


Figs 87.64–69. Immature stages of Anthomyzidae: (64) anterior part of third-instar larva of *Quametopia terminalis* (Loew), lateral view; (65) same, ventral view; (66) same, posterior part (caudal segment) of third-instar larva, lateral view; (67) same, ventral view; (68) right posterior spiracle of puparium of *Paranthomyza nitida* (Meigen), ventral view; (69) same, caudal view. Figs 64–67 (Roháček & Barber 2011, figs 64–67), Figs 68, 69 (Roháček 2009, figs 133, 134).

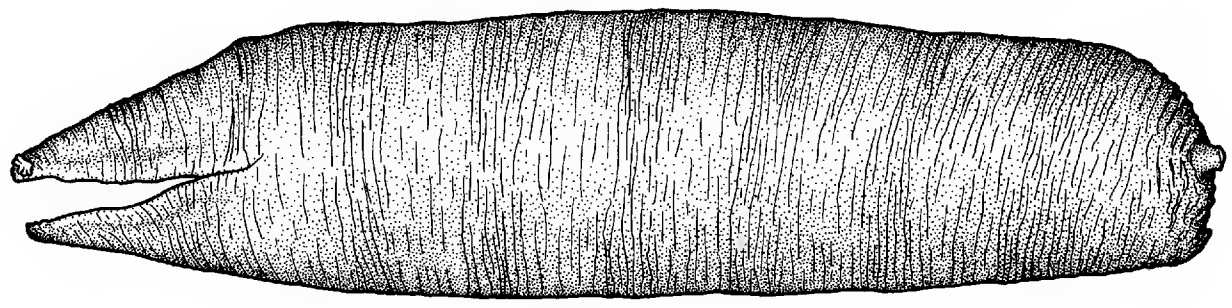
Abbreviations: an – anus; ant – antenna; cephsk – cephaloskeleton; cir – cirri; msth – mesothorax; p spr – posterior spiracle; prth – prothorax; prth spr – prothoracic spiracle; psceph – pseudocephalon.

***Margdalops* Roháček & Barraclough** (Anthomyzinae)**.** An endemic genus of six named species, all described from East Africa, ranging from Kenya to South Africa, with the majority of species (4) known from Kenya. Some additional species await description, including one from Nigeria (Roháček & Barraclough 2003). *Margdalops* resembles and is related to *Amygdalops*, but differs in having the antennal arista ciliate (Fig. 7), the occiput with a pair of silvery micro-tomentose stripes, the dorsocentral setae inserted more anteriorly, the wing darkened along the anterior margin, the cell *dm* very narrow and short and vein M_4 long (Fig. 23) and the differently formed male and female terminalia, with the male cercus enlarged and strongly sclerotised (Fig. 33). Although the biology of *Margdalops* species is poorly known, collection data indicate that some species may be associated with indigenous forests. Adults appear to occur throughout the year and those of *M. venustus* Roháček & Barraclough, 2003 were reared from nests of Cape robin-chat, *Cossypha caffra* (L.), although larvae probably developed in plant material used by birds in construction of their nests. Named species can be identified using the identification key provided by Roháček & Barraclough (2003).

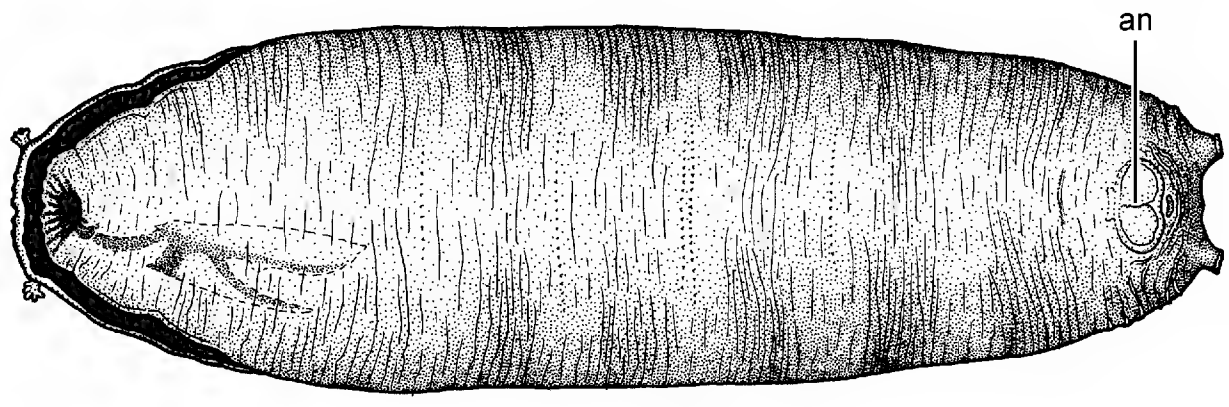
***Scelomyza* Séguy** (Anthomyzinae)**.** A monotypic genus originally described in the family Opomyzidae (Séguy 1938) and treated as such by Stuckenberg (1980: 635). More recently, examination of the unique female holotype of the type species, *S. hirticornis* Séguy, 1938, revealed that *Scelomyza* belongs to the family Anthomyzidae. Roháček (2014*a*) re-described the genus and species and suggested it to be likely related to *Apterosepsis*. The genus, which is only known from Kenya, is easily recognised by its peculiarly formed head (Fig. 9), with the shortened frons and the ocellar triangle reduced and shifted posteriorly; the uniquely long setose antennal postpedicel and enlarged postgena; combined with only 1 very strong frontoorbital seta (Fig. 9), the absence of acrostichal micro-setae on the thorax and the presence of a ctenidial spine on the fore femur (Fig. 18). The biology and immature stages of the species remain unknown with the only known specimen, the holotype, taken at an elevation of 2,100 m.



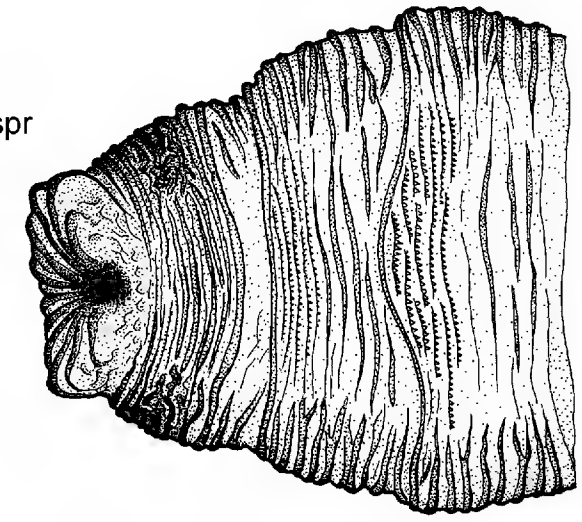
70 *Anagnota*



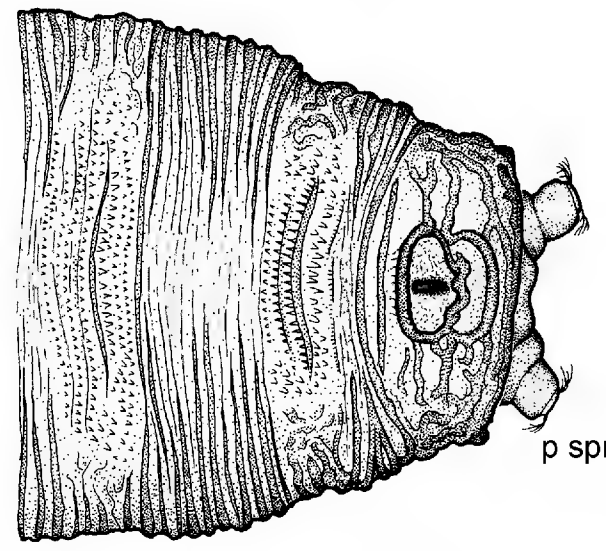
71 *Anagnota*



72 *Anagnota*



73 *Paranthomyza*



74 *Paranthomyza*

Figs 87.70–74. Immature stages of Anthomyzidae: (70) puparium of *Anagnota bicolor* (Meigen), dorsal view; (71) same, lateral view; (72) same, ventral view; (73) anterior part of puparium of *Paranthomyza nitida* (Meigen), ventral view; (74) same, posterior part of puparium, ventral view. Figs 70–72 (Roháček & Freidberg 1993, figs 26–28), Figs 73, 74 (Roháček 2009, figs 130, 131).

Abbreviations: an – anus; p spr – posterior spiracle; prth spr – prothoracic spiracle.

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AULACIGASTRIDAE 88

(Sap Flies)

Alessandra Rung and Wayne N. Mathis

Figs 88.1. Undetermined sex of *Aulacigaster africana* Barraclough (South Africa) (photograph © S.A. Marshall).

Diagnosis

[Based on *Aulacigaster*; the only genus in the region].

Small- to medium-sized acalyptrate flies (body length: 1.6–5.2 mm) (Fig. 1); colouration mostly dark brown to black; frons often bearing a transverse, large, orange fascia (Fig. 2) (Old and New World species), or with anterior ¼–½ yellowish in ground colour (New World species); mesonotum (Fig. 4) typically bearing micro-tomentum; wing membrane (Fig. 5) usually mostly hyaline, partly infuscate, with brown in some species.

Head (Figs 2–4) with face uniformly sclerotised, often protuberant (easily visible in lateral view); antenna with pedicel at most strongly sinuous dorsally, but not cap-like; postpedicel round to oval, forming an angle with pedicel or not; arista single articled, lacking basal articles, often with alternating dorsal and ventral branches (branches very tiny in some species, appearing bare under low magnification); ocellar setae, when present, minute; inner vertical setae typically slightly convergent, seta at most ¾ length of outer vertical seta; 2 fronto-orbital setae, posterior seta invariably reclinate, often medial to and almost aligned with anterior seta; 1–2 setulae between fronto-orbital setae, 1 proclinate; interfrontal seta absent; subvibrissal setae typically consisting of weaker setae posterior to vibrissa-like seta.

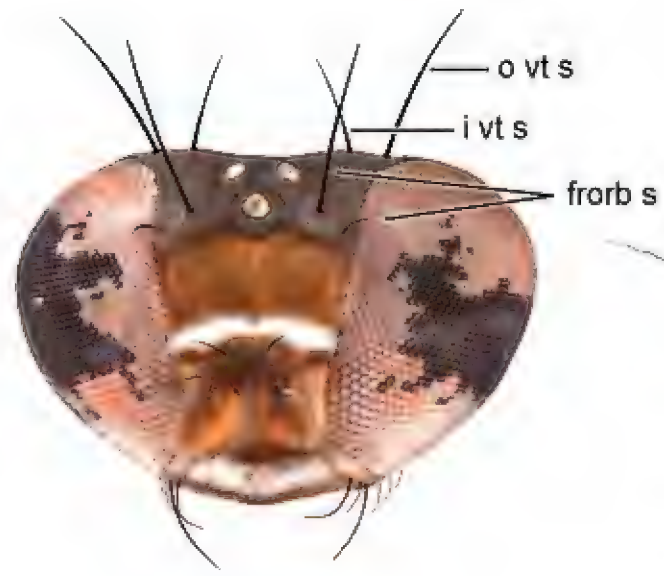
Thorax (Fig. 4) with anepisternum bearing 1–2 setae along posterior margin; 2 pairs of scutellar setae, apical pair of setae

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2021. Manual of Afrotropical Diptera. Volume 3. Brachycera—Cyclorrhapha, excluding Calyptratae. *Suricata* 8. South African National Biodiversity Institute, Pretoria; pp. 1957–1962.

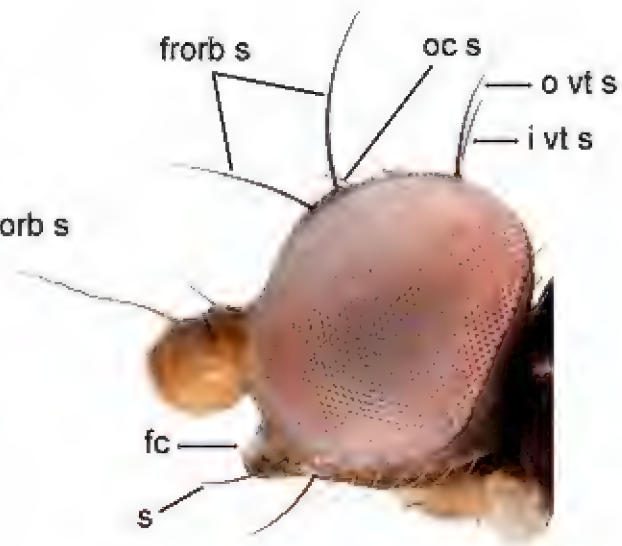
virtually parallel, slightly converging towards apex. Wing (Fig. 5) without costal breaks, at most costal vein (*C*) strongly weakened at apex of vein *Sc*; subcostal vein (*Sc*) partially fused with vein R_1 sub-apically, forming kink on vein R_1 in some species; crossvein *bm–m* absent, cells *bm* and *dm* confluent; cell *bm+dm* flat, lacking longitudinal crease or fold; crossvein *r–m* basal to middle of combined cell *bm+dm*.

Male abdomen (Figs 6, 7) with pregenital segment large, 2 × as long as tergite 5; male terminalia (Figs 6, 8–12) lacking surstylus, epandrium with rigid epandrial lobe; cerci separate or partially fused; subepandrial sclerite with caudal portion arching along edge of epandrium and proximal portion attached to hypandrial bridge; hypandrium bearing lateral, anterior postgonite; halves of hypandrium connected posteriorly by narrow bridge above phallapodeme, expanded ventrally, forming shovel-like structure, hypandrial halves connected anteroventrally, each bearing posterior lobe or projection and 1 to a few medial setae; phallapodeme wedge-shaped, with asymmetrical posterolateral projections; phallus short, partially sclerotised; female postabdomen (Fig. 13) distinctly shorter than preabdomen; tergite and sternite 7 separated; tergite 8 sometimes divided, dorsal connection membranous; sternite 8 often with strong submarginal setae; hypoproct with a few median, short setae; 3 sclerotised spermathecae (Fig. 14: 2 of 3 illustrated), globose to cylindrical.

Egg (Figs 15, 16) oval in dorsal and lateral views; longitudinally flattened, hatching strip demarcated by flanged edge; chorion covered with honeycomb reticulations and longitudinal ribs. Third-instar larva (Figs 17–21) sub-cylindrical, with amphipneustic respiratory system, bearing long, partially retractile

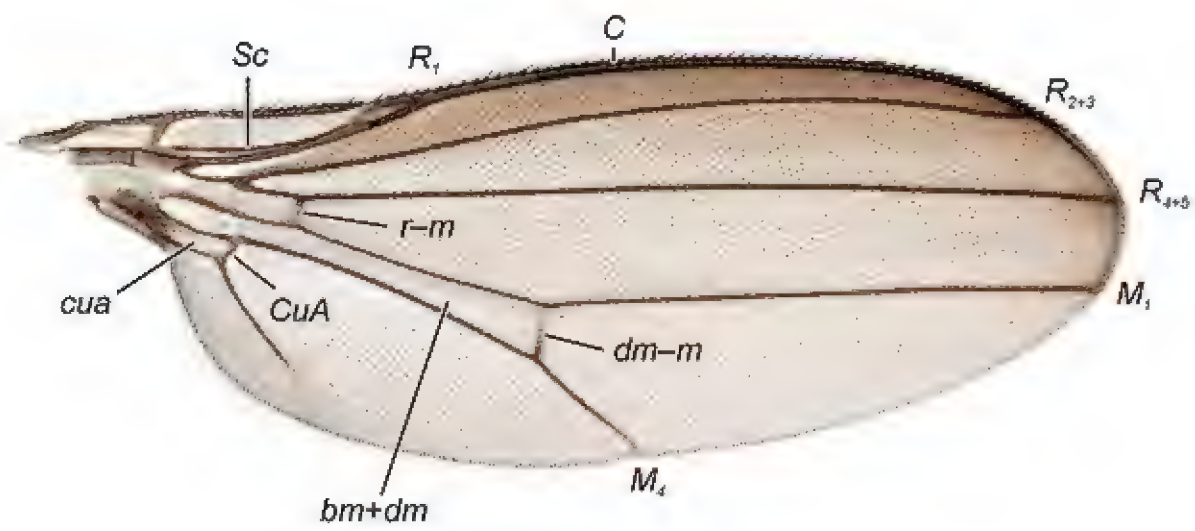


2 *Aulacigaster*



3 *Aulacigaster*

4 *Aulacigaster*



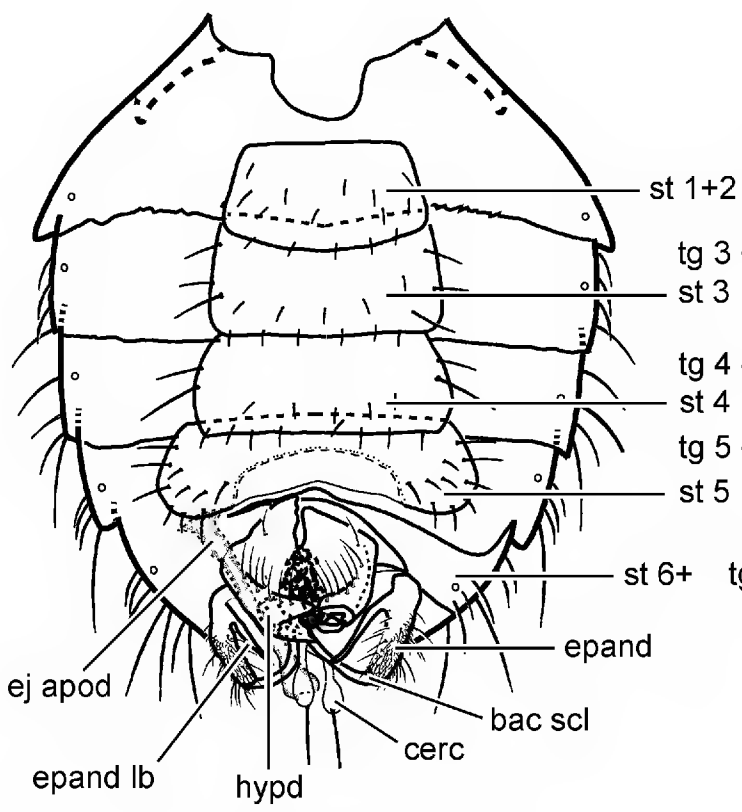
5 *Aulacigaster*

Figs 88.2–5. Male head, mesonotum and wing of Aulacigastridae: (2) head of *Aulacigaster africana* Barraclough, anterior view; (3) same, lateral view; (4) same, head and mesonotum, dorsal view; (5) same, wing, dorsal view.

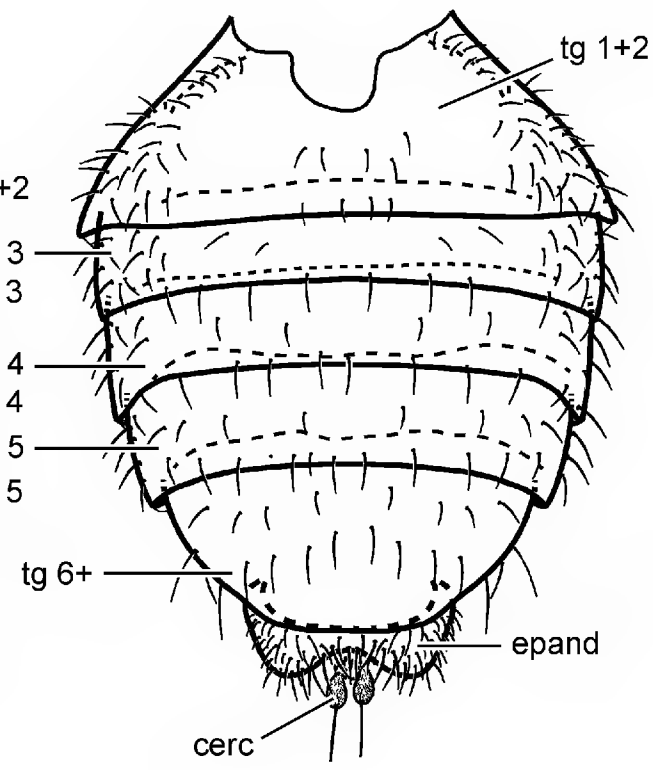
Abbreviations: *bm+dm* – basal medial cell + discal medial cell; *C* – costal vein; *CuA* – anterior branch of cubital vein; *cua* – anterior cubital cell; *dm–m* – discal medial crossvein; fc – face; frorb s – fronto-orbital setae; i vt s – inner vertical seta; M_1 – first branch of media; M_4 – fourth branch of media; o vt s – outer vertical seta; oc s – ocellar seta; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; s - seta; *Sc* – subcostal vein.

terminal respiratory siphon (Fig. 17); integument white, virtually transparent, clothed in minute spicules and sensory setae or smooth; cephaloskeleton (Figs 19, 20) slender, with well-developed mouthhooks, bearing 2 pairs of accessory teeth; intermediate and basal sclerites separate; 3 thoracic and 8 abdominal segments distinct; abdominal segments with ventral creeping welts bearing minute spicules; abdominal segment 8 with small anal pad (Fig. 17); prothoracic spiracles (Fig. 21) small, retracted into pair of deep, narrow pockets; posterior spiracles at apex of long respiratory siphon, joined at their bases, bifurcating posteriorly; puparium (Figs 22, 23) pale brown, oval in shape, with prothoracic spiracle completely everted.

Adult Aulacigastridae are readily distinguishable from Periscelididae (see Chapter 91) and Anthomyzidae (see Chapter 87) genera by the chaetotaxy of the head (Figs 2–4) (ocellar seta greatly reduced to absent, postvertical seta absent, 2 fronto-orbital setae); the sclerotised, protruding face (also in



6 *Aulacigaster* ♂



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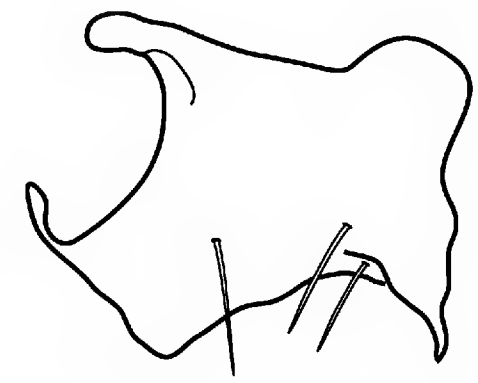

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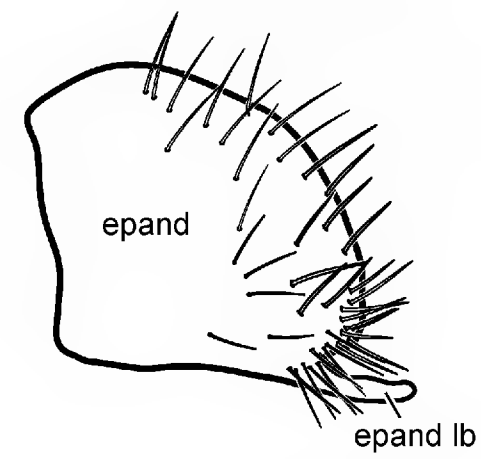

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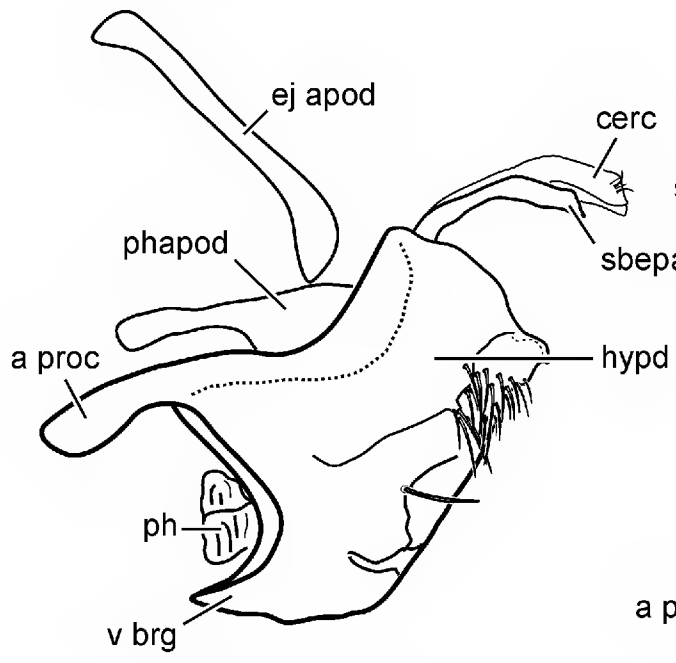

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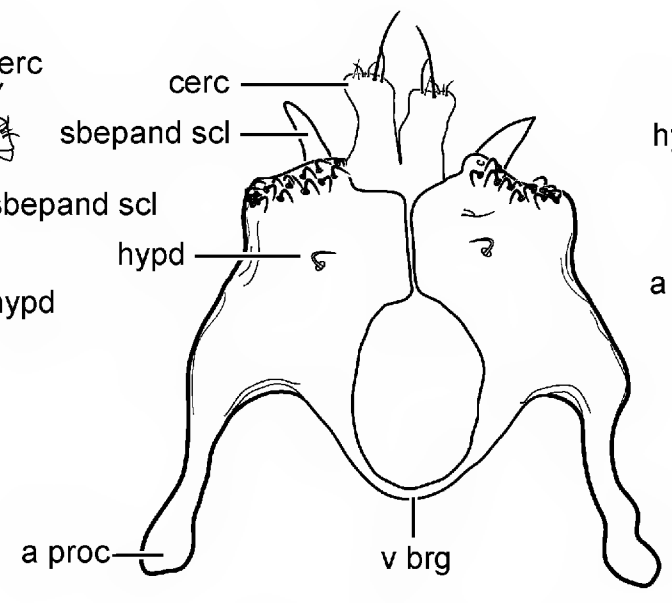

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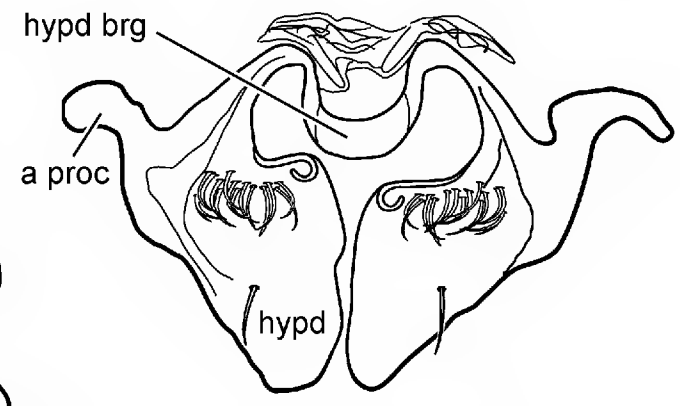


12 *Aulacigaster* ♂

Figs 88.6–12. Male abdomen and terminalia of Aulacigastridae: (6) abdomen of *Aulacigaster africana* Barraclough, ventral view; (7) same, dorsal view; (8) hypandrium of *A. freidbergi* Rung & Mathis, lateral view; (9) same, epandrium, lateral view; (10) internal male terminalia of *Aulacigaster neoleucopeza* Mathis & Freidberg, lateral view (epandrium removed) (non-Afrotropical); (11) same, hypandrium, subepandrial sclerite and cerci, ventral view; (12) same, hypandrium, posterior view. Figs 8–12 (Rung & Mathis 2011, figs 166, 167, 178, 180, 181).

Abbreviations: a proc – anterior process; bac scl – bacilliform sclerite; cerc – cercus; ej apod – ejaculatory apodeme; epand – epandrium; epand lb – epandrial lobe; hypd – hypandrium; hypd brg – hypandrial bridge; ph – phallus; phapod – phallapodeme; sbepand scl – subepandrial sclerite; st – sternite; tg – tergite; v brg – ventral bridge.

Periscelididae); the antennal pedicel not cap-like (also in Anthomyzidae); and wing venation (crossvein *r–m* basal to middle of combined cell *bm+dm*; crossvein *bm–m* absent; cells *bm* and *dm* confluent) (Fig. 5).

Biology and immature stages

Information in the literature on the natural history of *Aulacigaster* Macquart species is scarce. Adults and immatures from the Nearctic and Palaearctic Regions are peculiar to weeping wounds and sap fluxes of deciduous trees (Ferrar 1987: 79; Robinson 1953; Teskey 1976). A group of Neotropical species inhabits bromeliads (Rung & Mathis 2011). Larvae of these species develop inside the bromeliad cups (Bromeliaceae), which tend to be filled with rainwater. In addition, some adults of Neotropical *Aulacigaster* species have been collected on freshly cut logs. Numerous adults of multiple species have also been collected by sweeping between the shaded buttresses of *Ceiba* (Malvaceae) trees in the Neotropics. A few species have been collected on Heliconiaceae leaves (Rung & Mathis 2011).

Little has been published on the biology of Afrotropical aulacigastrids. *Aulacigaster africana* Barraclough, 1993, was originally collected from a shaded sandstone ledge (Barraclough 1993) adjacent to low, south-easterly facing montane forest, on the banks of the Tugela River, KwaZulu-Natal Province, South Africa. Additional specimens have been attracted to hanging traps baited with fermenting fruit-bait (A.H. Kirk-Spriggs, pers. comm. 2013). Another species, *A. borbonica* Hilger & Kassebeer, 2000, was collected on Réunion Is., from a slime flux of the Horsetail tree, *Casuarina cunninghamiana* Miq. (Casuarinaceae) – an Australian plant introduced to the island. *Aulacigaster borbonica* was also observed ovipositing on the slime flux, but larvae were not found (Hilger & Kassebeer 2000).

Immatures stages have been described for *A. africana* (Papp 2008), *A. bromeliae* Rung & Mathis, 2011 (Rung & Mathis 2011), *A. falcata* Papp, 1988 (Papp 1988) and *A. leucopeza* (Meigen, 1830) (Robinson 1953).

Economic significance

The Aulacigastridae have no economic importance. There are no records involving any species in agricultural, medical, veterinary or forensic works.

Classification

The family Aulacigastridae belongs to the superfamily Opomyzoidea (McAlpine 1989: 1454) and the family's sister-group, according to McAlpine's phylogeny (1989: 1455), is the family Periscelididae. Characterisation of Aulacigastridae differs widely among authors (see below) and up to five genera have been assigned to it, in addition to the nominate genus, *Aulacigaster*. Aulacigastridae *sensu stricto* include only one other genus, *Curiosimusca* Rung, Mathis & Papp, from the Oriental Region, representing an addition to what recent authors (Hilger & Kassebeer 2000; Kassebeer 2001; Mathis & Freidberg 1994; Papp 1997; Rung & Mathis 2011), have included in their characterisations of the family. A broader characterisation includes the genera *Cyamops* Melander, *Planinasus* Cresson and *Stenomicra* Coquillett and also a fossil species from Baltic amber, *Protoaulaciga sterelectra* Hennig, 1965.

Hennig (1958, 1965, 1969, 1971) first advocated this broader definition, followed by Griffiths (1972: 211, with the exclusion of *Stenomicra*), Teskey (1987: 76) and McAlpine (1989: 1463). McAlpine (1978, 1983) proposed a rather different characterisation that: (1) transferred the genera *Cyamops*, *Planinasus* and *Stenomicra* from Aulacigastridae to Periscelididae; (2) excluded *P. electrus* Grimaldi & Mathis, 1993 from Aulacigastridae; and (3) described two new genera in the family, *Ningulus* McAlpine (Afrotropical Region) and *Nemo* McAlpine (Australasian Region). Freidberg (1994) erected the family Neminidae for *Ningulus*, *Nemo* and his new Afrotropical genus *Nemula*. Freidberg's work resulted again in a monotypic Aulacigastridae. *Protoaulaciga sterelectra* was most recently listed in Aulacigastridae by Evenhuis (1994: 423) and Roháček (1998) tentatively transferred *Echidnocephalodes barbatus* (Lamb, 1914) (Seychelles) from the Anthomyzidae to the Aulacigastridae. This placement has not been generally adopted and the writers believe that it warrants further scrutiny within the context of a phylogenetic analysis.

Identification

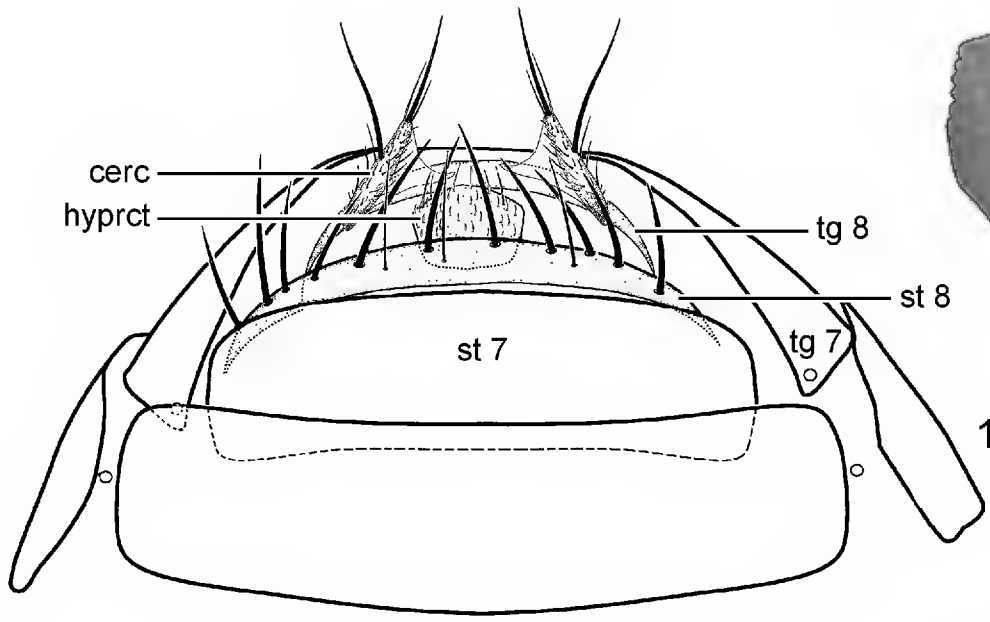
Aulacigastridae, as defined here, are a distinct family based on adult characters. Two genera are currently recognised, *Aulacigaster* (see "Synopsis of the fauna" below) and *Curiosimusca*, which includes only three Oriental species (Rung *et al*. 2005).

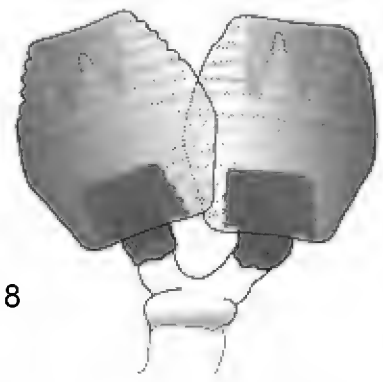
Species of the *leucopeza*-group, the only group of species represented in the Afrotropical Region, are best separated based on characters of the male terminalia. Additionally, infuscation of the wing membrane, the size of the shiny macula on the vertex of the head between the ocellar triangle and the eye margin, size and shape of the orange macula on the vertex, presence of anterior dorsocentral setae, length of the palpus and colouration of legs can also be used. Aulacigastridae are best micro-pinned in the field for later double-mounting (see Chapter 2).

Synopsis of the fauna

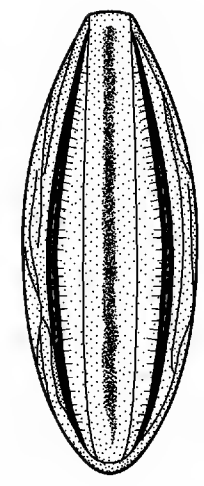
Aulacigastridae include 57 species globally in two genera: *Aulacigaster* and *Curiosimusca*. *Aulacigaster* is the more speciose and widely distributed of the two and the only genus recorded from the Afrotropical Region.

***Aulacigaster* Macquart.** A genus of 55 described species, occurring in the Afrotropical, Nearctic, Neotropical, Oriental and Palaearctic Regions. The genus was recently revised by Rung & Mathis (2011), who divided it into five species-groups. Of these, only the *A. leucopeza*-group occurs outside of the Neotropics. Five species are known from the Afrotropical Region distributed in Cameroon, Malawi, Réunion Is., South Africa and Zambia (see Rung & Mathis 2011, map 14). The current number of species known from the Afrotropics is likely a fraction of the actual diversity of the genus in the region. An identification key to all five Afrotropical species was provided by Rung & Mathis (2011).

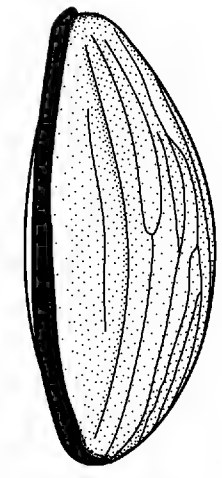




14 *Aulacigaster* ♀



15 *Aulacigaster*



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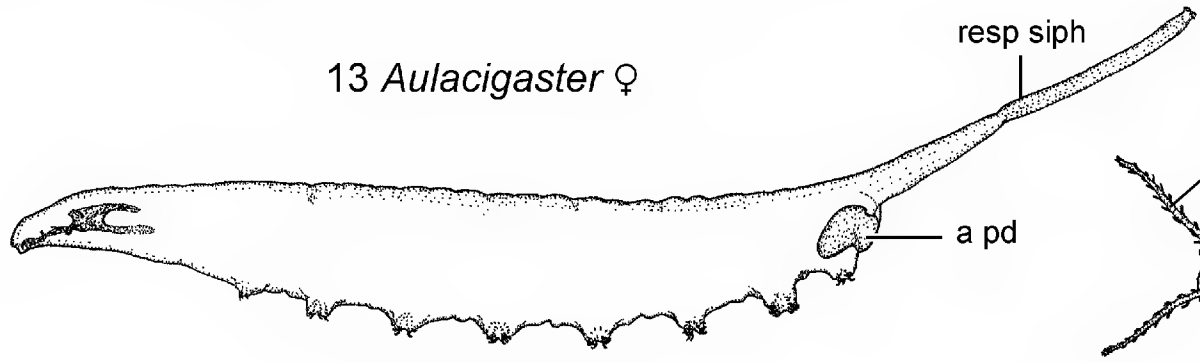
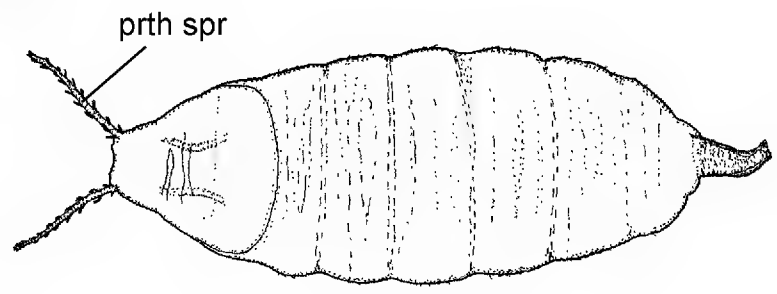
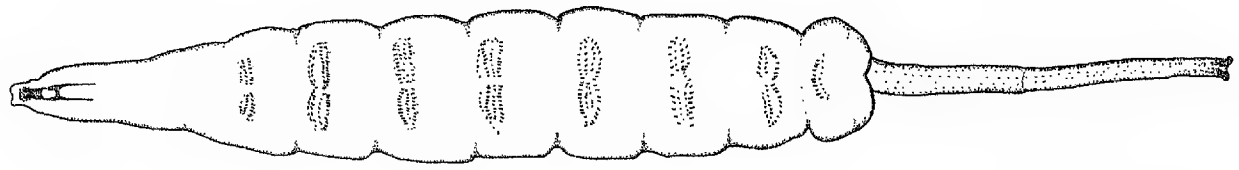


13 *Aulacigaster* ♀

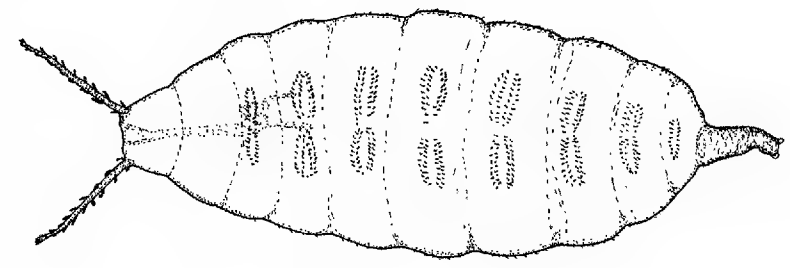


22 *Aulacigaster*

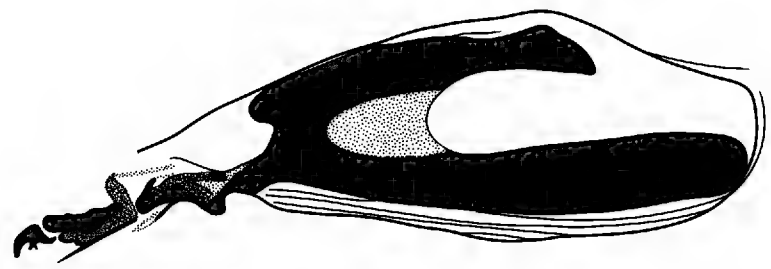
17 *Aulacigaster*



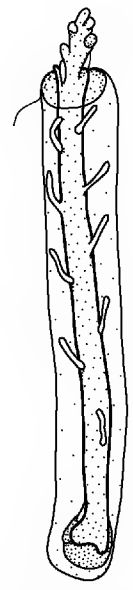
18 *Aulacigaster*



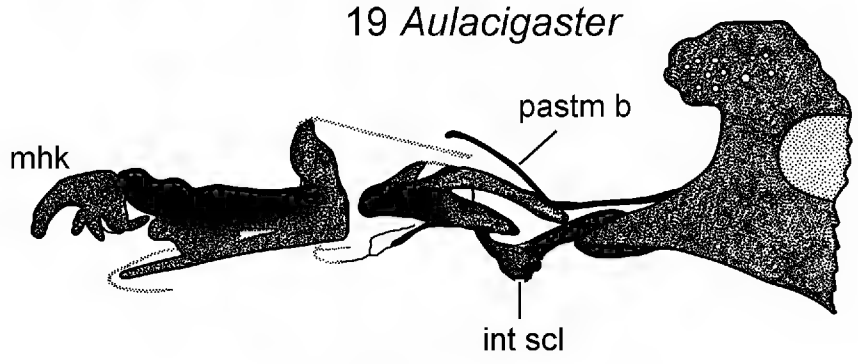
23 *Aulacigaster*



19 *Aulacigaster*



21 *Aulacigaster*



20 *Aulacigaster*

Figs 88.13–23. Female postabdomen and immature stages of Aulacigastridae: (13) female postabdomen of *Aulacigaster africana* Barraclough, ventral view; (14) same, two of three spermathecae; (15) same, egg, dorsal view; (16) same, lateral view; (17) habitus of third-instar larva of *Aulacigaster falcata* (Papp), lateral view (non-Afrotropical); (18) same, ventral view; (19) same, cephaloskeleton, lateral view; (20) same, cephalic part at higher magnification; (21) same, prothoracic spiracle, lateral view; (22) same, habitus of puparium, dorsal view; (23) same, ventral view. Figs 13, 14, 17, 18, 22, 23 (Papp 1998, figs 9, 10, 12, 15, 19, 20), Figs 19, 20 (after Papp 1998, figs 17, 18), Figs 15, 16 (after Papp 2008, figs 3, 4).

Abbreviations: a pd – anal pad; cerc – cercus; hyprct – hypoproct; int scl – intermediate sclerite; mhk – mouthhook; pastm b – parastomal bar; prth spr – prothoracic spiracle; resp siph – respiratory siphon; st – sternite; tg – tergite.

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NEMINIDAE 89

(Nobody Flies)

Amnon Freidberg†

Fig. 89.1. *Nemula longarista* Freidberg (Madagascar) (photograph © S.A. Marshall).

Diagnosis

Small-sized (body length: 1.0–2.1 mm), winged acalyptrate flies (Fig. 1); colouration varies from predominantly yellow to predominantly black, but more or less elaborate and contrasting pattern usually present on some or all major body parts.

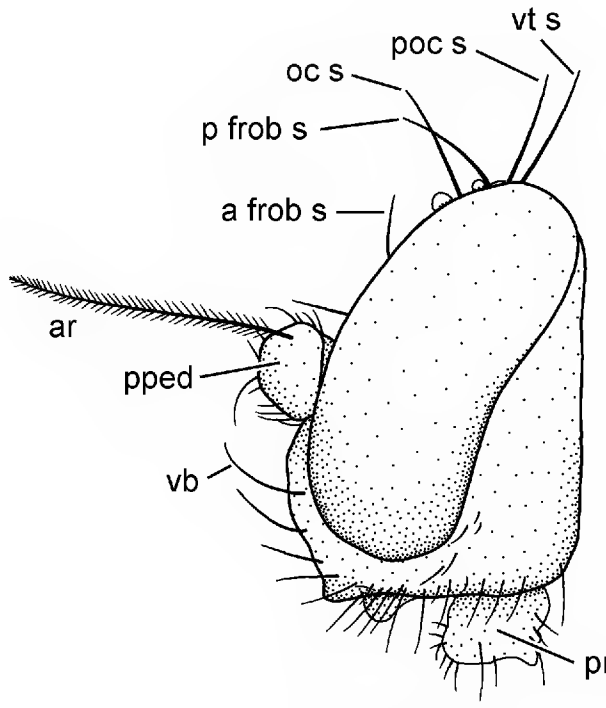
Head (Figs 2–6) usually higher than long, more or less oval in lateral view, with eye distinctly higher than long (Fig. 2); in *Ningulus* McAlpine head rectangular in lateral view and head and eye distinctly longer than high (Fig. 4); frons without interfrontal vittae, or frontal vittae indistinct, but with pair of convergent interfrontal setae near ptilinal fissure (Fig. 3) and 0–2 short to long fronto-orbital setae (Fig. 2), sometimes intermixed with and indistinguishable from several additional setulae (*Ningulus*, Fig. 5); ocellar setae well-developed or reduced to about same size as fronto-orbital setulae (Fig. 2); postocellar setae divergent (*Nemula* Freidberg, Fig. 3), parallel (*Nemo* McAlpine, Fig. 6), or convergent (*Ningulus*, Fig. 5); 1 distinct vibrissa present, although mostly appearing as anterodorsal-most seta of genal row (Figs 2, 4); antenna short, with postpedicel more or less rounded or short oval (Figs 2, 3), arista well-developed, 3-articled, usually about as long as head, sometimes (*Nemula longarista* Freidberg, 1994) *ca* 2.5 × as long as head, with short, but distinct dense dorsal and ventral branches (Figs 2, 3); proboscis short (Figs 2, 4).

Thorax (Figs 7, 8) with 1–2 dorsocentral setae; posterior dorsocentral seta sometimes (*Nemula*, Fig. 7) displaced laterally and accompanied by an anterior row of *ca* 6 setulae; acrostichal setae absent, except in non-Afrotropical *Nemo centriseta* McAlpine, 1983 (Fig. 8); acrostichal setulae either absent or forming 1 pair of rows (Fig. 7); pleura, except katepisternum,

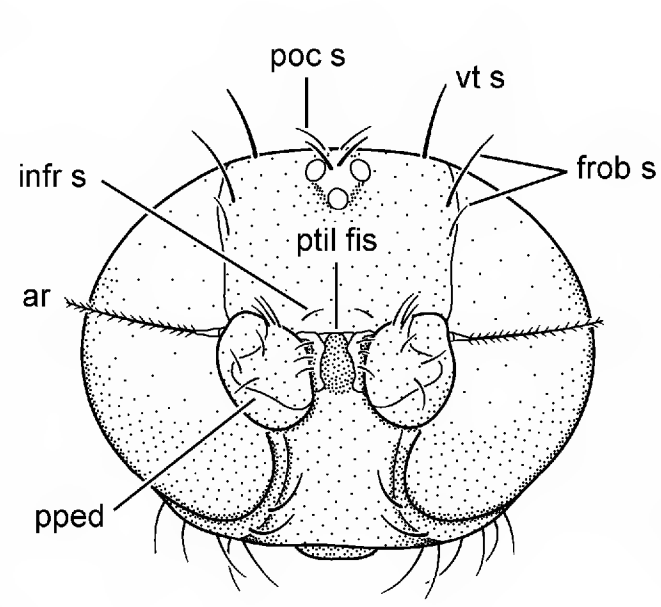
Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2021. Manual of Afrotropical Diptera. Volume 3. Brachycera—Cyclorrhapha, excluding Calyptratae. *Suricata* 8. South African National Biodiversity Institute, Pretoria; pp. 1963–1969.

without setae; anepisternum bare (in *Ningulus* and *Nemo*) or with 1 setula (in *Nemula*); anepimeron with 1 or more setulae; prosternum much longer than wide. Scutellum convex, usually with 2 pairs of marginal setae; basal seta slightly or distinctly shorter than apical seta or absent; apical seta erect. Wing (Figs 9–11) with membrane entirely hyaline (in some *Ningulus* and *Nemo*) or with brown pattern, especially over or in vicinity of cell r_1 (*Nemula*); sclerotised part of subcostal vein (*Sc*) reaching far less than ½ distance from humeral crossvein (*h*) to subcostal break (in *Nemula* subcostal vein entirely de-sclerotised and barely discernible; Fig. 9); subcostal break present or lacking; third costal sector (between end veins R_1 and R_{2+3}) 0.5–1.0 × as long as fourth costal sector (*Nemo*, Fig. 10), or about 0.25–0.30 × as long (*Nemula*, Fig. 9 and *Ningulus*, Fig. 11); longitudinal veins generally straight (*Nemo*) or strongly or moderately bent and distinctly change orientation at intersections with crossveins *r–m* and *dm–m* (*Nemula*); cells *dm* and *bm* partially (*Nemo*) or entirely (*Nemula*) confluent; crossvein *r–m* situated beyond middle of compound cell *dm+bm*; cell *dm+bm* > ½ as wide as cell m_1 at level of crossvein *dm–m*. Legs usually without overt features; terminal tarsal segment subtriangular, depressed.

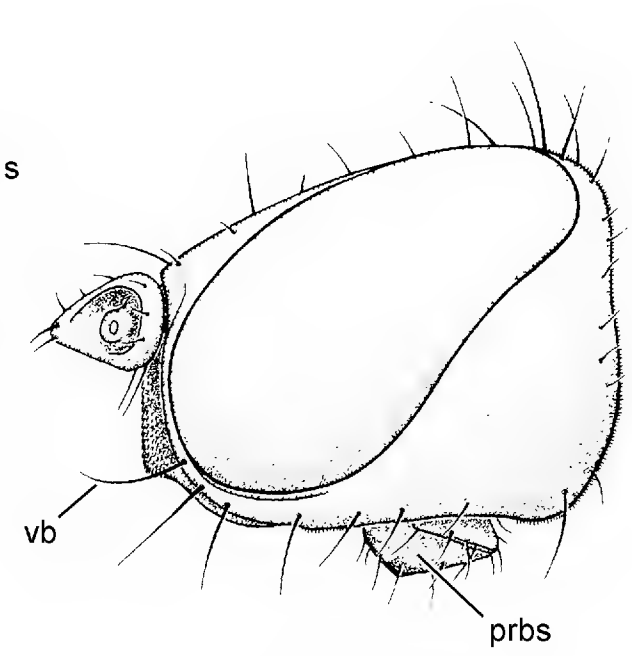
Abdomen of male with 5 segments, with at least 5 pairs of spiracles, all but one in membrane; female with 4 preabdominal segments (Fig. 16), with 6 pairs of spiracles in membrane; male terminalia (Figs 12–15) with epandrium (Fig. 12) slightly asymmetrical, without bacilliform sclerites; surstylus (Fig. 12) loosely articulated with epandrium; distiphallus (Figs 13–15)



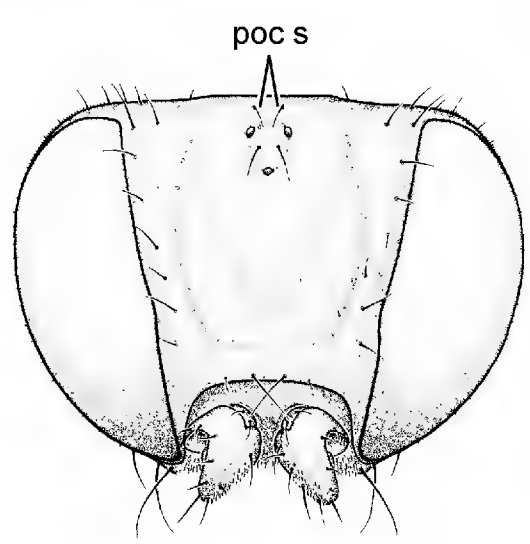
2 *Nemula*



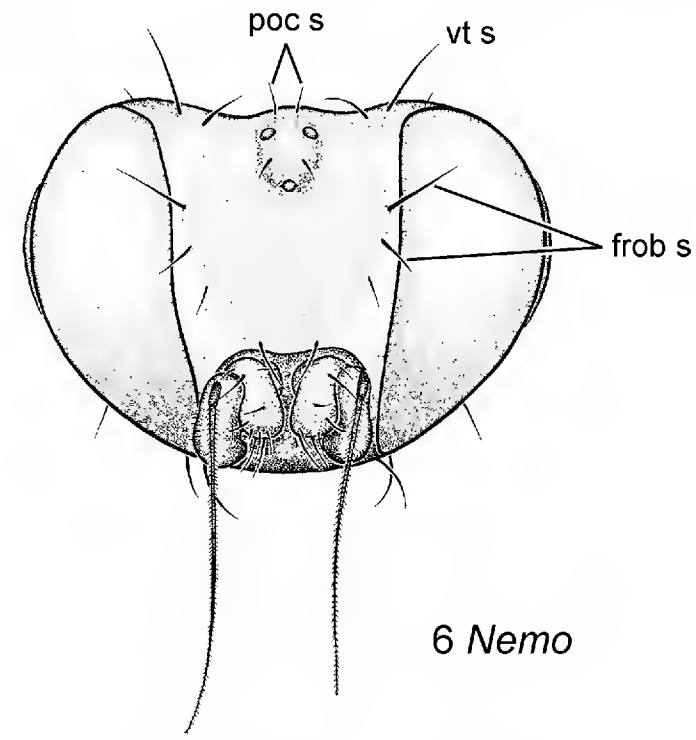
3 *Nemula*



4 *Ningulus*



5 *Ningulus*



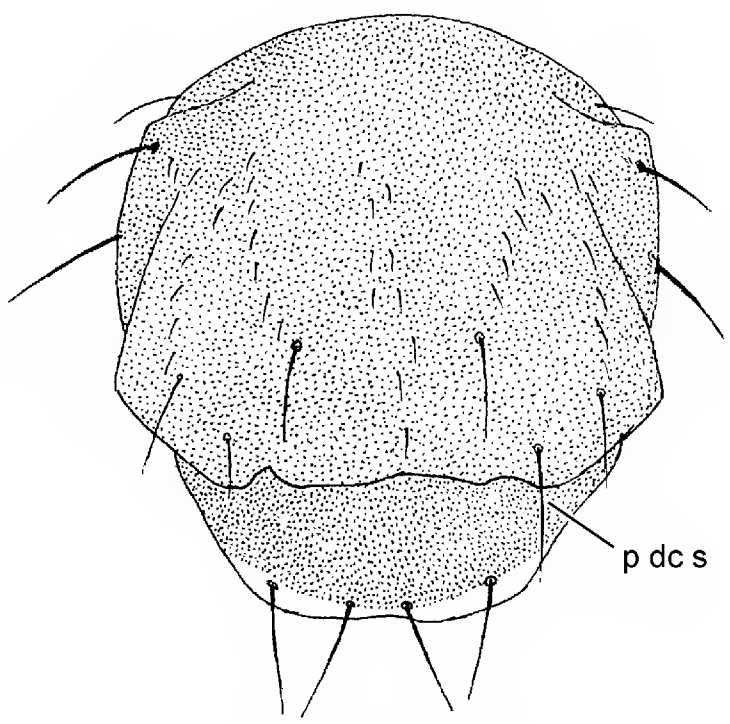
6 *Nemo*

Figs 89.2–6. Heads of Neminidae: (2) *Nemula major* Freidberg, lateral view; (3) *N. longarista* Freidberg, anterior view (distal ⅔ of aristae not illustrated); (4) *Ningulus simatus* McAlpine, lateral view; (5) same, dorsal view; (6) *Nemo kentae* McAlpine, dorsal view (non-Afrotropical). Figs 2, 3 (after Freidberg 1994, figs 6, 1, respectively), Figs 4–6 (McAlpine 1983, figs 5, 4, 7, respectively).

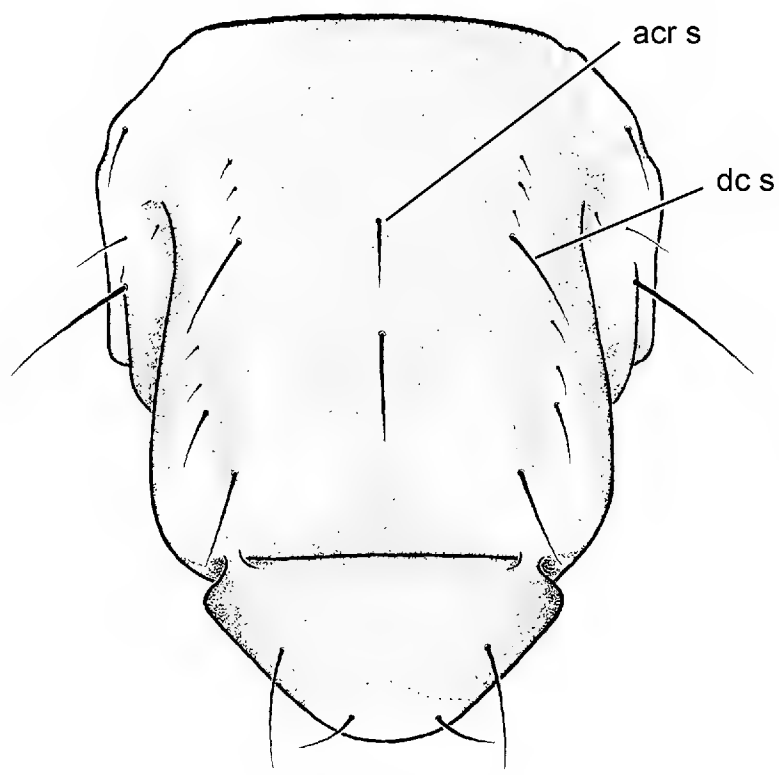
Abbreviations: a frob s – anterior fronto-orbital seta; ar – arista; frob s – fronto-orbital seta; infr s – interfrontal seta; oc s – ocellar seta; p frob s – posterior fronto-orbital seta; poc s – postocellar seta; pped – postpedicel; prbs – proboscis; ptil fis – ptilinal fissure; vb – vibrissa; vt s – vertical seta.

long, asymmetrical, curved, usually densely spinose (Figs 13, 14), but not spinose in *Nemula* (Fig. 15); ejaculatory apodeme greatly reduced or absent; female terminalia (Figs 16–19) with postabdomen telescopic, largely membranous, about as long as preabdomen when extended (Fig. 16); 2 spermathecae present, either spherical or cup-shaped (Fig. 17), or with 3 sclerotised globules serially attached to each other (Fig. 18); ventral receptacle formed of sclerotised bifid structure (Fig. 19).

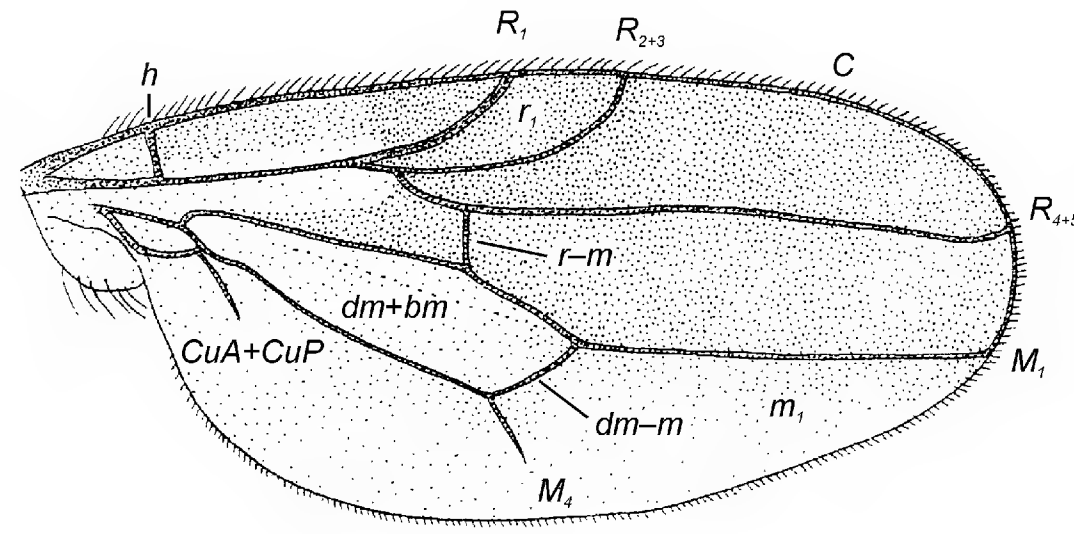
Adult Neminidae may be confused with Neurochaetidae (see Chapter 90), due to the general habitus and in sharing the same or similar ecological niches. They are also related and somewhat similar to Periscelididae (e.g., *Stenomicra* Coquillett) (see Chapter 91) and Aulacigastridae (see Chapter 88) and are superficially similar, especially in the form of the short antenna and long, setulose arista, to some Chloropidae, but lack a carinate proepisternum (see Chapter 96) and Sphaeroceridae,



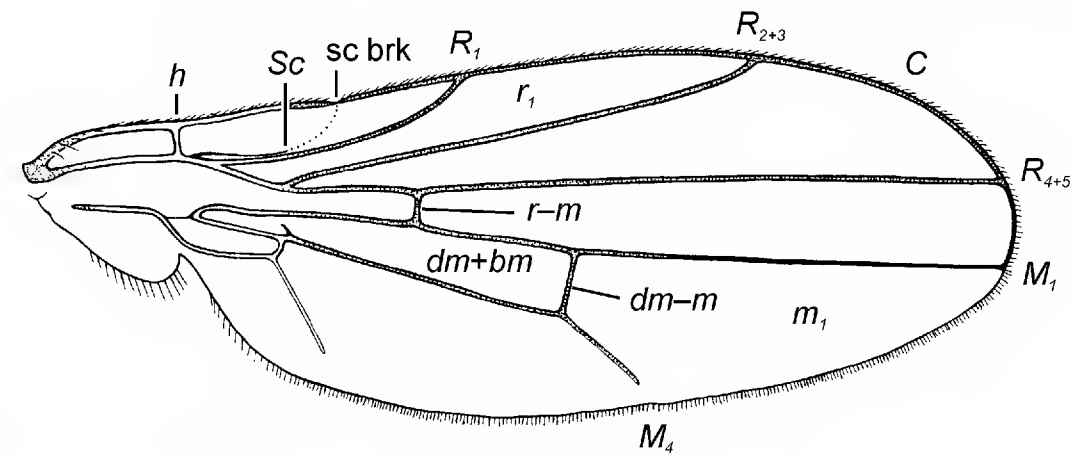
7 *Nemula*



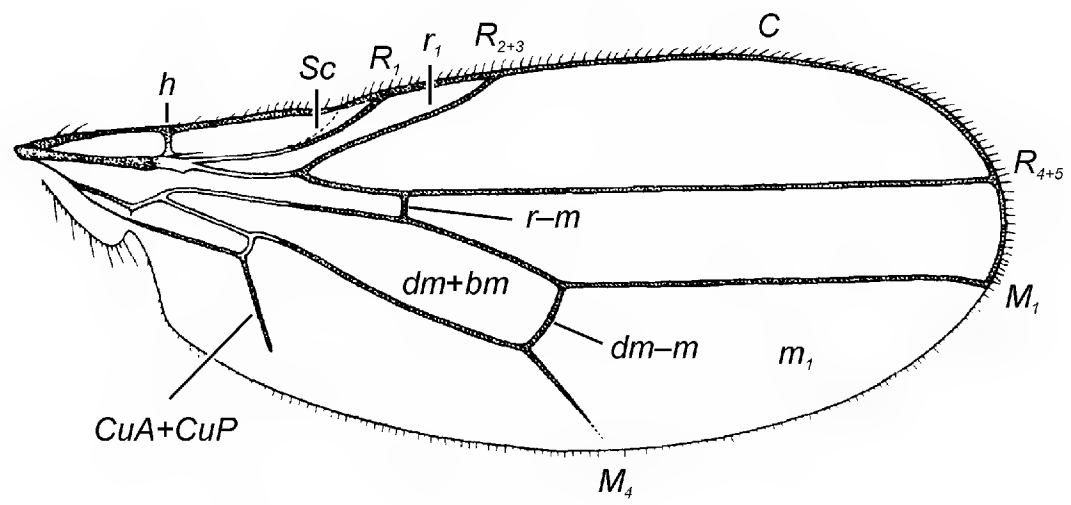
8 *Nemo*



9 *Nemula*



10 *Nemo*



11 *Ningulus*

Figs 89.7–11. Thoraces and wings of Neminidae (dorsal views): (7) thorax of *Nemula major* Freidberg; (8) same, *Nemo centriseta* McAlpine (non-Afrotropical); (9) wing of *Nemula major*; (10) same, *Nemo corticeus* McAlpine (non-Afrotropical); (11) same, *Ningulus simatus* McAlpine. Figs 7, 9 (Freidberg 1994, figs 9, 12), Figs 8, 10, 11 (McAlpine 1983, figs 9, 15, 19).

Abbreviations: acr s – acrostichal seta; *C* – costal vein; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; dc s – dorsocentral seta; *dm+bm* – discal medial cell + basal medial cell; *dm–m* – discal medial crossvein; *h* – humeral crossvein; M_1 – first branch of media; m_1 – first medial cell; M_4 – fourth branch of media; p dc s – posterior dorsocentral seta; R_1 – anterior branch of radius; r_1 – first radial cell; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Sc* – subcostal vein; sc brk – subcostal break.

but lack an enlarged metatarsal segment on the hind leg (see Chapter 99).

Biology and immature stages

Nothing is known regarding the biology of Neminidae, except that adults of some species have been collected off the leaves of monocotyledons, particularly *Alocasia* (Araceae), *Ravenala madagascariensis* Sonn. and *Strelitzia* (both Strelitziaceae).

Immature stages have not been studied, except for the egg of *Nemula longarista*, obtained by dissecting the abdomen of a pinned female. The egg (Fig. 20) is elongate-oval, 0.4 × 0.14 mm, with conspicuous, crater-like micropyllar end, packed with seta-like projections (Fig. 20, inset). The corium is mostly smooth, but centrally with distinct reticulation composed of pentagonal or rounded cells (Fig. 20, inset).

Economic significance

Neminidae have no known economic significance.

Classification

The taxonomic history of this family is short and rather straightforward. It was first described by McAlpine (1983) as a subfamily of Aulacigastridae and originally included the new genera *Nemo* from Australia and *Ningulus* from South Africa. In 1985, McAlpine added a new species of *Nemo* from Papua New Guinea. Freidberg (1994) described a third genus, *Nemula*, with three new species, all from Madagascar, and in the same paper, raised the subfamily to family-level. Barraclough (1999) described a second species of *Ningulus* from Zimbabwe and two new species of *Nemo* from South Africa. Thus, the Afrotropics is the only region that is home to all three genera of the family.

The Neminidae belong to the superfamily Opomyzoidea *sensu* McAlpine (1989: 1464). They have mostly been treated by the above-mentioned authors as part of, or closely related to, the Aulacigastridae, but there has not been a comprehensive study on the relationships between Neminidae and other families within the Opomyzoidea, as done by McAlpine (1989) for other families. A partial treatment of this kind, with a mere mention of the Neminidae, is available in the Aulacigastridae chapter (see Chapter 88) in this *Manual* (Rung & Mathis 2021: 1960) and will not be repeated here. Within the Opomyzoidea *sensu* McAlpine, however, the Neminidae appear to be most closely related to a clade comprising Aulacigastridae + Periscelididae + Neurochetidae. The Neminidae is here regarded as the sister family to Aulacigastridae and these two families together may be the sister-group to Periscelididae, with Neurochetidae being the next kin. According to Wiegmann *et al.* (2011), Neminidae are the sister-group to the Neotropical Inbiomyiidae and both families are close to the Nerioidea + Aulacigastridae complex, while Neurochetidae are placed distantly on the phylogenetic tree. This interpretation does not match the morphological data and should be reconsidered.

Identification

Identification keys to genera and/or species are included in each of the four existing publications on the Neminidae (sometimes as Nemininae) (Barraclough 1999; Freidberg 1994 and McAlpine 1983, 1985). Barraclough (1999) presented the most recent identification key to genera, although this does not include the genus *Nemula*. Freidberg's (1994) publication, although focusing on *Nemula*, includes all three genera. Neminidae are best micro-pinned in the field for later double-mounting (see Chapter 2).

Key to genera of Afrotropical Neminidae

1. Head (Fig. 4) strongly depressed, distinctly longer than high, with numerous, short fronto-orbital setae or setulae; thorax with anterior notopleural seta inserted more dorsally than posterior notopleural seta; postalar seta present; scutellum with 2–4 pairs of setae; apical spur of hind tibia short, but strong . . . . . *Ningulus* McAlpine

– Head (e.g., Fig. 2) not depressed, about as high as long or distinctly higher than long, with 1–2 fronto-orbital setae (e.g., Fig. 2), at least 1 seta long; thorax with posterior notopleural seta inserted more dorsally than anterior notopleural seta; postalar seta absent; scutellum with 2 pairs of setae; apical spur of hind tibia weak 2

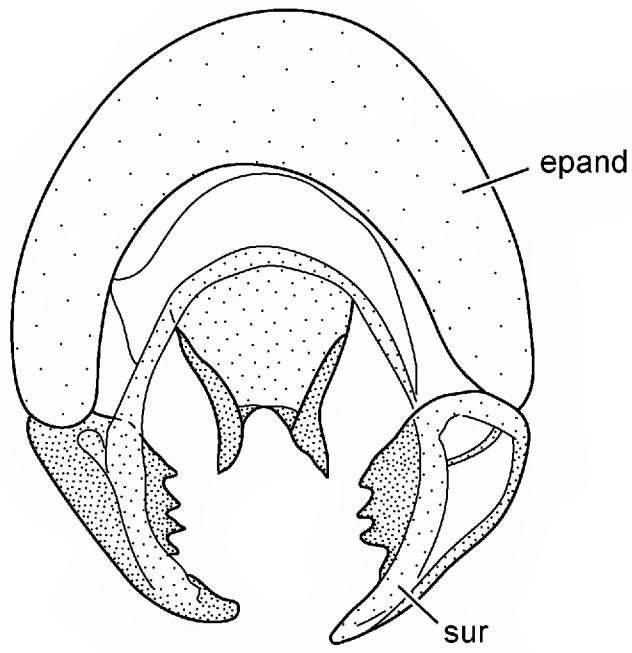
2. Wing (Fig. 10) with third costal sector (between veins R_1 and R_{2+3}) 0.5–1.0 × as long as fourth sector (between veins R_{2+3} to R_{4+5}); subcostal vein (*Sc*) sclerotised basally, clearly discernible; vein M_1 generally straight, without bend at intersection with crossvein *dm–m*; all forks of radial vein (*R*) in proximal ⅓ of wing; cell *dm+bm* narrow, almost parallel-sided and truncate apically; head (Fig. 6) with 2 vertical setae and 2 long fronto-orbital setae, the anterior proclinate and the posterior reclinate . . . . *Nemo* McAlpine

– Wing (Fig. 9) with third costal sector (between veins R_1 and R_{2+3}) 0.16–0.35 × as long as fourth sector (between veins R_{2+3} to R_{4+5}); subcostal vein (*Sc*) entirely de-sclerotised, barely discernible; vein M_1 strongly bent at intersection with crossvein *dm–m*; all forks of radial vein (*R*) in median ⅓ of wing; cell *dm+bm* strongly widened to level of crossvein *r–m*; crossvein *dm–m* strongly oblique, resulting in distantly pointed cell *dm+bm*; head (Figs 2, 3) with 1 vertical seta and 1 long, reclinate or proclinate fronto-orbital seta, occasionally with additional anterior reclinate seta . . . . . *Nemula* Freidberg

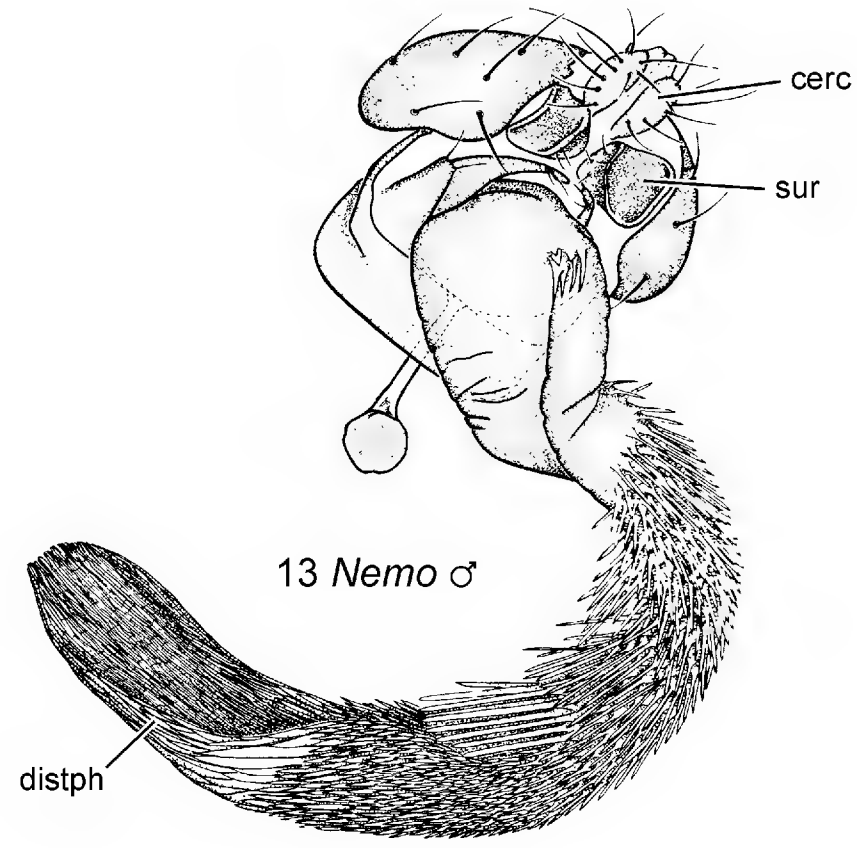
Synopsis of the fauna

Fifteen species in three genera of this small family are recorded from the Southern Hemisphere of the Old World, with all three genera and seven species recorded from the Afrotropical Region.

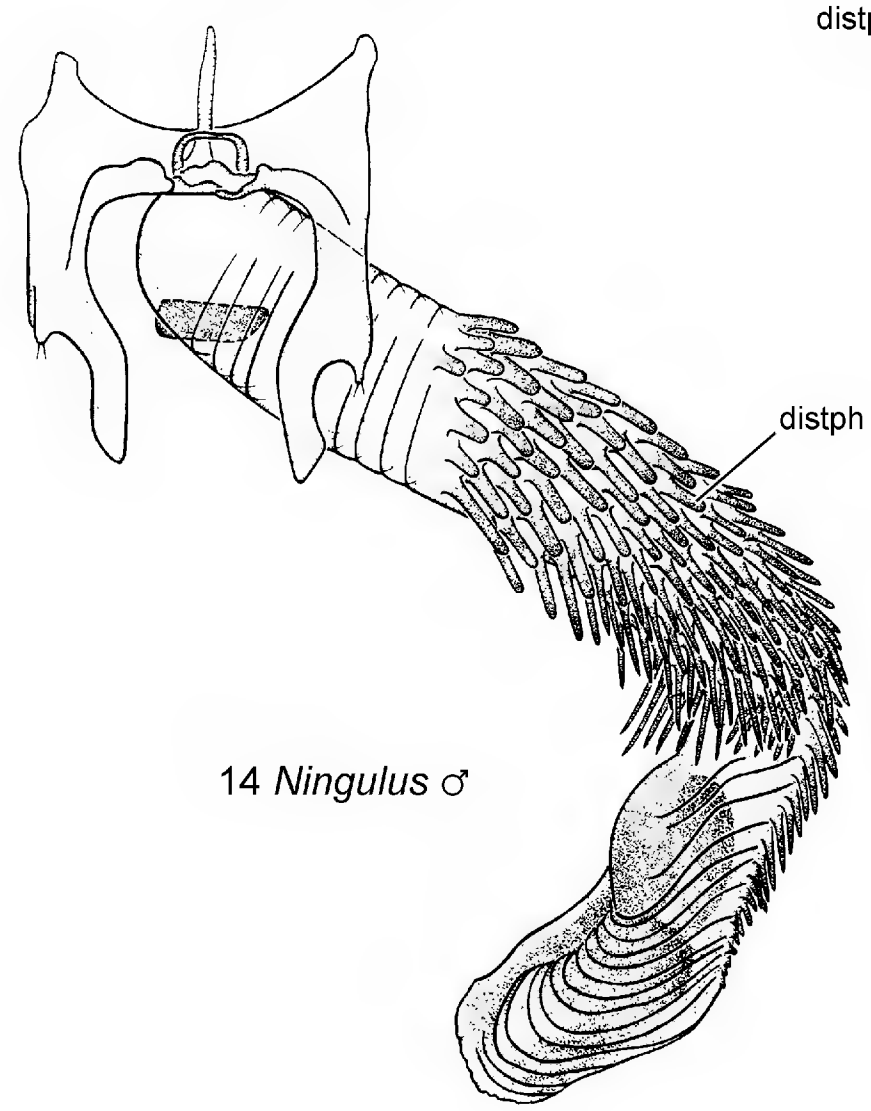
***Nemo* McAlpine.** A genus of 10 described species, occurring in the Afrotropical and Australasian Regions (Australia and Papua New Guinea), with two species in the Afrotropics and additional species expected to occur in the region. *Nemo* is the only known genus in the family to occur outside the limits of the Afrotropical Region. *Nemo capensis* Barraclough, 1999



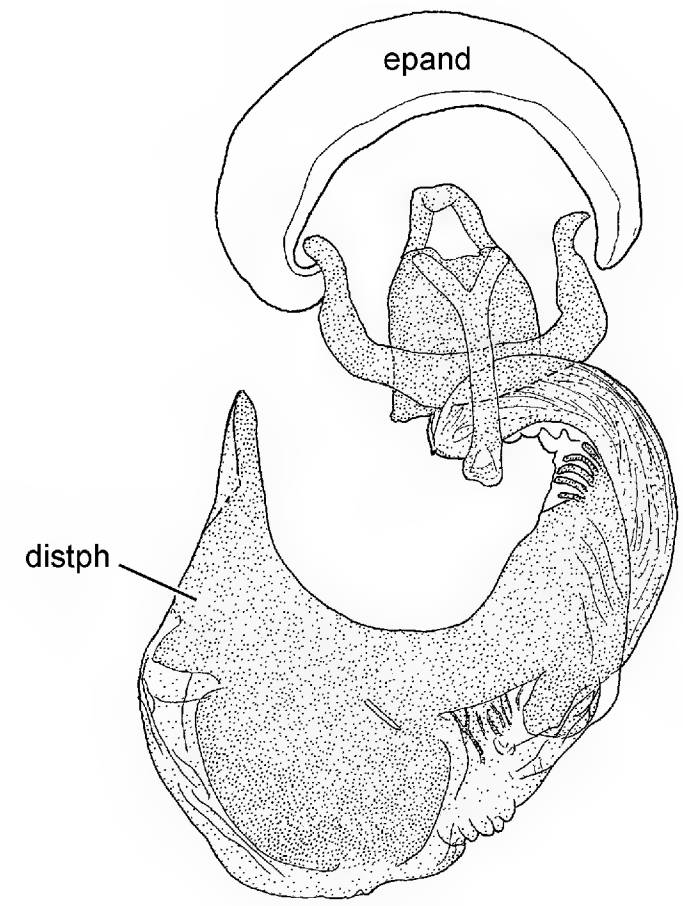
12 *Nemula* ♂



13 *Nemo* ♂



14 *Ningulus* ♂



15 *Nemula* ♂

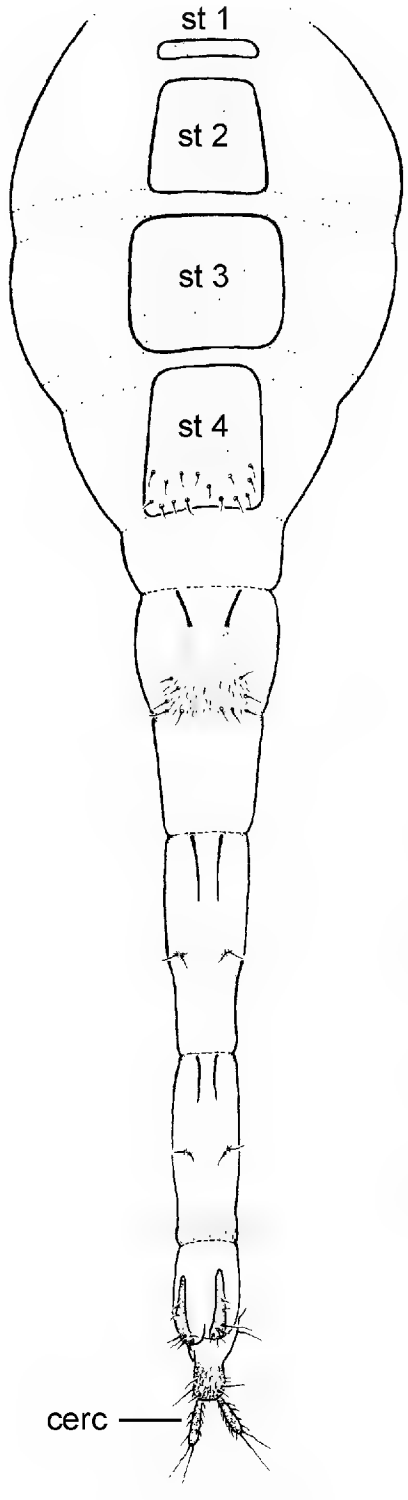
Figs 89.12–15. Male terminalia of Neminidae: (12) *Nemula longarista* Freidberg, posterior view; (13) distiphallus and associated structures of *Nemo phaeotylos* McAlpine, ventral view (non-Afrotropical); (14) same, *Ningulus simatus* McAlpine, dorsal view; (15) same, *Nemula longarista*. Figs 12 (after Freidberg 1994, fig. 15), Fig. 15 (Freidberg 1994, fig. 14), Figs 13, 14 (McAlpine 1983, figs 28, 20, respectively).

Abbreviations: cerc – cercus; distph – distiphallus; epand – epandrium; sur – surstylus.

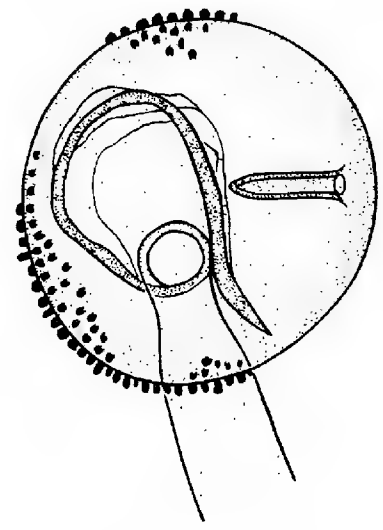
is recorded from the south-west of the Eastern Cape Province and *N. zuluensis* Barraclough, 1999 from the north of KwaZulu-Natal Province (both South Africa); the latter species is recorded from the leaves of *Strelitzia nicolai* (Regel & Koern) (Strelitziaceae) (Barraclough 1999). The biology and immature stages otherwise remain unknown. An identification key to the two Afrotropical species was provided by Barraclough (1999).

***Ningulus* McAlpine.** An endemic genus of two described species, confined to Southern Africa and additional species are expected to occur in the region. *Ningulus simatus* McAlpine, 1983 is recorded from the Eastern Cape, South Africa and *N. macalpinei* Barraclough, 1999 from the Chimanimani Mountains in eastern Zimbabwe; the latter species is recorded from the leaves of *Strelitzia nicolai* (Barraclough 1999). The biology and immature stages otherwise remain unknown. An identification key to the two species was provided by Barraclough (1999).

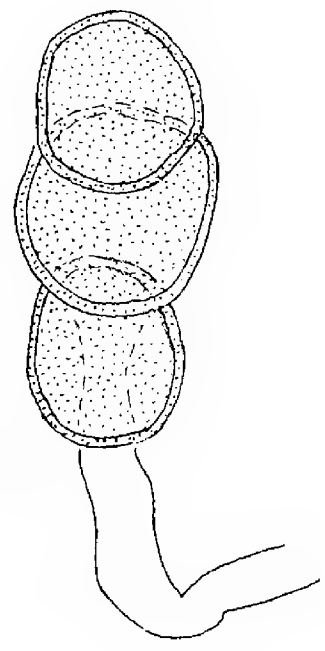
***Nemula* Freidberg.** An endemic genus of three described species, *N. argentata* Freidberg, 1994, *N. longarista* and *N. major* Freidberg, 1994, which are confined to Madagascar. Additional undescribed species are expected to occur on the island. One species occurs in the north, one in the central part and one in the south. Two of the species were collected on *Ravenala madagascariensis* (Strelitziaceae) and adults of *N. longarista* were swarming on the undersides of leaves (Freidberg 1994). The biology and immature stages otherwise remain unknown. An identification key to the three species was provided by Freidberg (1994).



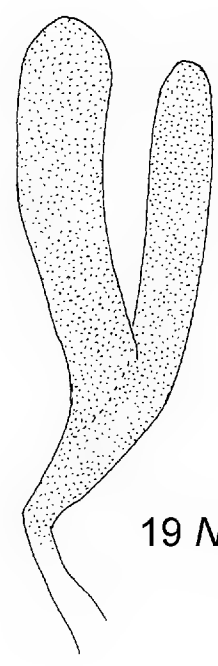
16 *Nemo* ♀



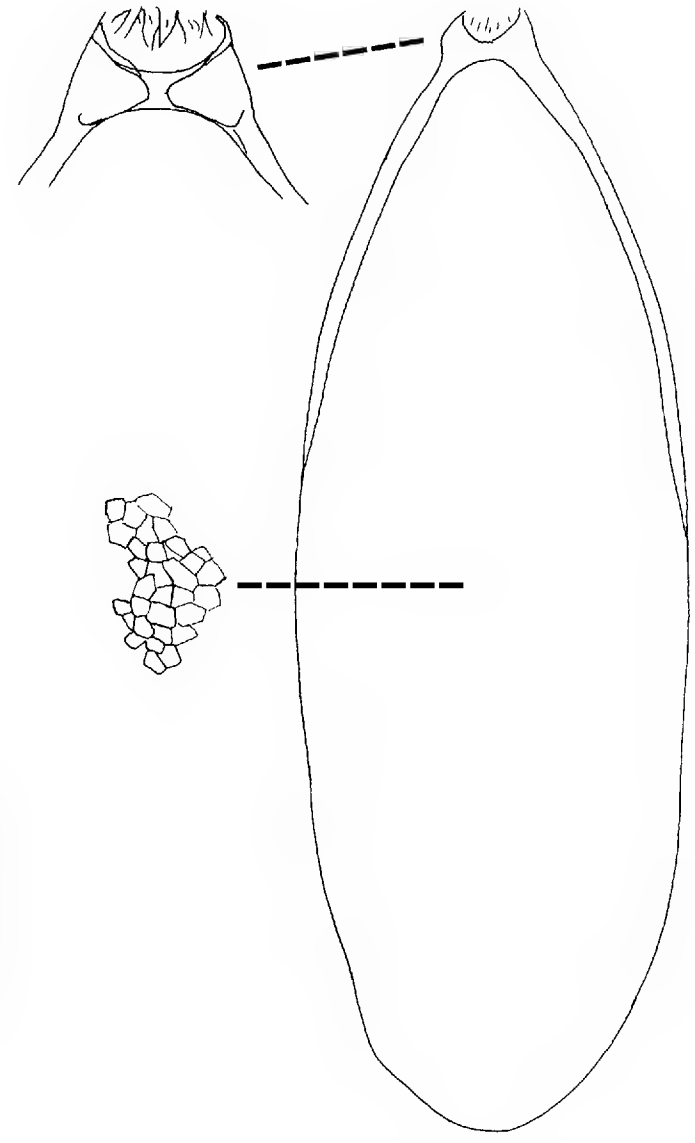
17 *Nemo* ♀



18 *Nemula* ♀



19 *Nemula* ♀



20 *Nemula*

Figs 89.16–20. Female abdomen, terminalia and egg of Neminidae: (16) extended pre- and postabdomen of *Nemo corticeus* McAlpine, ventral view (non-Afrotropical); (17) spermatheca of *N. centriseta* McAlpine, lateral view (non-Afrotropical); (18) same, *Nemula longarista* Freidberg; (19) same, ventral receptacle, lateral view; (20) same, egg, lateral view (insets: detail of chorion surface and micropyle). Figs 16, 17 (McAlpine 1983, figs 16, 23), Figs 18–20 (Freidberg 1994, figs 18–20).

Abbreviations: cerc – cercus; st – sternite.

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NEUROCHAETIDAE 90

(Upside-down Flies)

Owen Lonsdale

Fig. 90.1. Male of *Neurochaeta inversa* McAlpine (non-Afrotropical) (photograph © S.A. Marshall).

Diagnosis

Extant species, excluding the unusual Australian genus *Nothoasteia* Malloch (McAlpine 1993, 2011), can be diagnosed as follows:

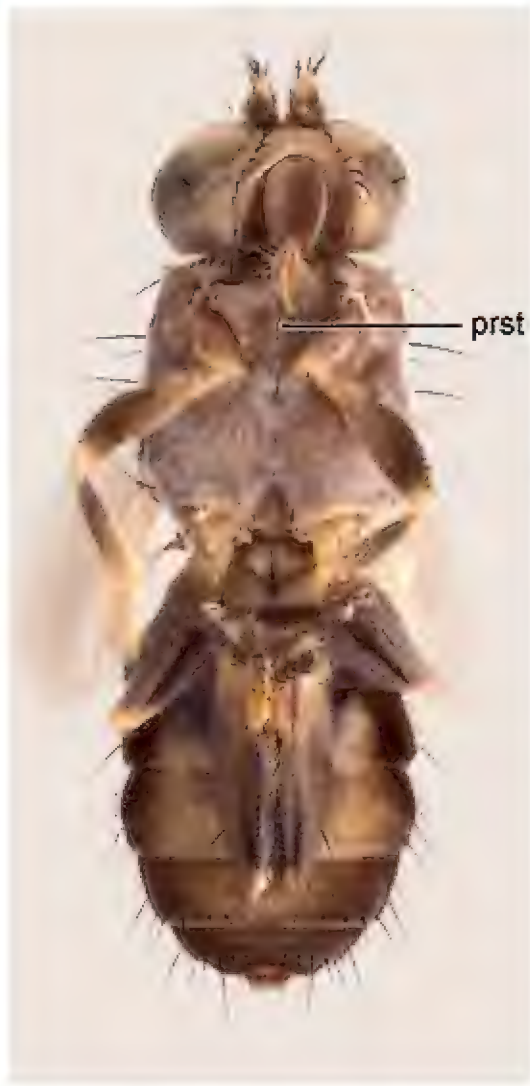
Small-sized acalyptrate flies (body length: *ca* 1.9–5.8 mm) (Figs 1–4), slightly or strongly compressed dorsoventrally, at least dorsally on notum (Fig. 4); body brown to dark brown, with venter, head and legs often paler, but sometimes with more extensive yellow markings, or mostly yellow to white; most of body clothed in micro-pubescence that may be partially silvery tomentose (usually on head, subscutellum and epandrium), or velvety, with only limited sections of thorax sometimes shiny; setae and setulae dark brown to black or yellow, often with colour of setae heterogeneous; wing with limited infuscation, or more broadly clouded, sometimes excluding section at or near wing base.

Head with antenna decumbent; pedicel large, cap-like, with wide seam on outer-distal surface that encompasses much of smaller, narrower and subovate postpedicel (Figs 6–8); pedicel

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2021. Manual of Afrotropical Diptera. Volume 3. Brachycera—Cyclorrhapha, excluding Calyptratae. *Suricata* 8. South African National Biodiversity Institute, Pretoria; pp. 1971–1979.

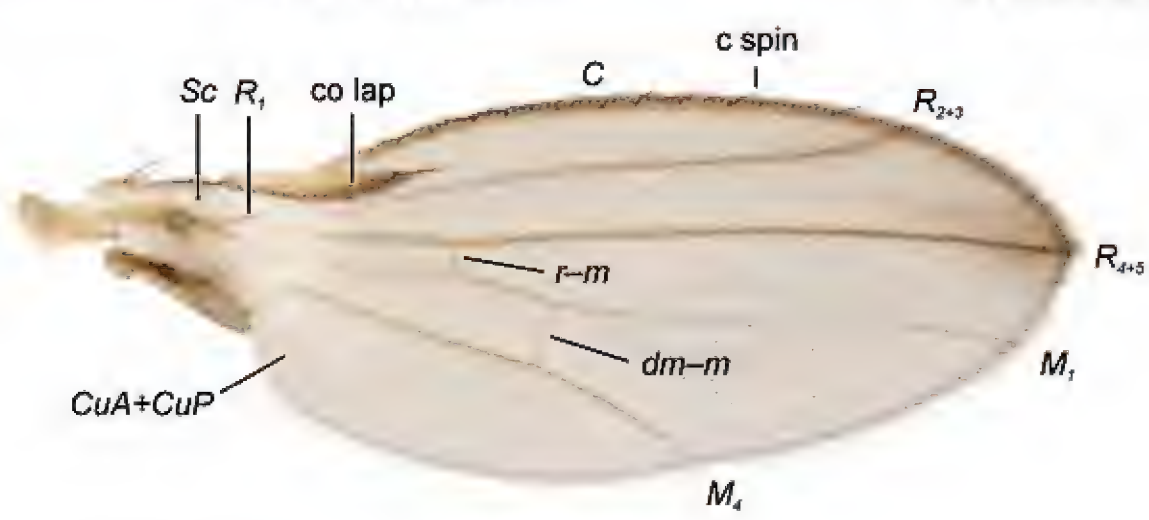
often with stout setae along inner-distal and sometimes outer-distal margins; arista usually bipectinate (Figs 7, 8), sometimes short-plumose (*Neurocytta* McAlpine) (Fig. 6), or pubescent; eye broadly to narrowly oval, oblique (Figs 4, 6, 7); face often well-sclerotised, sometimes appearing soft, often convex (at least ventrally and/or dorsally along midline, similar to some Ephydridae (see Chapter 100) and Periscelididae (see Chapter 91)), sometimes narrowed medially due to encroaching eye margins; gena narrow, relatively short, often slightly produced and upcurved anteriorly; postgena relatively large, wedge-shaped, with venter often bulbous; palpus small, subcylindrical to laterally flattened and spatulate; vibrissa and 2–6 vibrissa-like subvibrissal setae present (Figs 6, 7), sometimes interspersed by smaller setulae; usually 3–4 fronto-orbital setae, with first (anterior-most), or second pair inset and inclinate (similar to *Czernyola* Bezzi, Clusiidae) (see Chapter 81) and sometimes shifted anteriorly past level of true anterior seta, which may also be inclinate; orbital setulae scattered, short;

2 *Neurotexis* ♂



3 *Neurotexis* ♂

4 *Neurotexis* ♂



5 *Neurotexis* ♂

Figs 90.2–5. Habitus and wing of Neurochaetidae: (2) habitus of *Neurotexis freidbergi* McAlpine, dorsal view ♂; (3) same, ventral view; (4) same, lateral view; (5) wing of *N. delphis* McAlpine, dorsal view ♂.

Abbreviations: *C* – costal vein; c lap – costal lappet; c spin – costal spinules; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *dm–m* – discal medial crossvein; M_1 – first branch of media; M_4 – fourth branch of media; prst – prosternum; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Sc* – subcostal vein; sbsctl – subscutellum.

ocellar setae short, diverging; postocellar setae small and parallel to slightly divergent when present; inner vertical seta sometimes absent; postgena usually with strong seta below eye (homology of seta across genera uncertain, treated as "suborbital" and "postgenal" seta in McAlpine (1978, 1988a)).

Thorax slightly to conspicuously flattened; pleuron angled inwards on katepisternum and also below notal suture, but usually only anterior to midpoint of anepisternum with remainder vertical; meron and posterior region of anepimeron recessed. Scutellum usually relatively short; subscutellum small (*Neurocytta*), or much enlarged, exceeding apical margin of scutellum and sometimes obliterating much of mediotergite; subscutellum often silvery tomentose if enlarged (Figs 2, 4); fore and hind coxal bridges absent; prosternum reduced, usually linear (Fig. 3); chaetotaxy: 1 postpronotal; 2 notopleural; proepisternal usually 0 (small in some *Neurotexis* McAlpine); 0 posterior intra-alar; 0–1 presutural seta and 0–2 postsutural supra-alar; 1 or 2 dorsocentral (sometimes small or barely differentiated from setulae); 1 or 2 katepisternal; 0 anepisternal; 1 postalar; setulae on disc of notum numerous, seriate, or irregularly positioned; katepisternum and sometimes venter of anepisternum variably setulose; Afrotropical species with 1 pair of apical scutellar setae (closely spaced in *Neurocytta*) and either 1 pair of lateral setae (*Neurotexis*), or 1 short row of setulae (*Neurocytta*); *Neurochaeta* McAlpine (Australasian) with 2–7 pairs of additional marginal scutellar setae and sometimes enlarged setulae. Wing well-developed (Figs 4, 5), sometimes slightly reduced with alula, anal cell, crossvein *bm–m* and/or vein *CuA+CuP* atrophied; costal vein (*C*) extending to veins M_1 or R_{4+5}; only subcostal break present; costal spinules pronounced to indistinct; costal vein sometimes produced into lappet at break (*Neurotexis*) (Fig. 5); subcostal vein (*Sc*) weakened apically, usually incomplete, sometimes only reaching costal vein as a fold; vein R_{4+5} ending at, or very near wing apex, which may be slightly pointed; veins R_{4+5} and M_1 sub-parallel, sometimes slightly convergent; sometimes veins R_1 and R_{4+5} with 2–4 dorsal setulae (absent in *Neurotexis*). Legs with hind femur and sometimes fore femur relatively stout; mid leg reduced in size and hind leg at least slightly enlarged and elongate (Figs 3, 4); fore coxae widely separated, sometimes slightly compressed and carinate; mid coxae separated, sometimes only narrowly so; hind coxae approximate; fore femur with row of posteroventral setae, 1 row of shorter posterodistal setae and 1 group of sometimes seriate posterodorsal setae; mid femur sometimes with anteroventral seta/e medially; hind femur with at least 1 anteromedial seta, at least 1 dorsal seta and sometimes row of ventrobasal to ventromedial setae; fore and mid tibiae with small dorsoapical seta; mid tibia sometimes with ventroapical seta; hind tibia sometimes with stouter distoventral setulae and sometimes (*Neurocytta*) with 2 medial anterodorsal setae.

Abdomen usually dorsally flattened (Figs 2–4); sternites nearly as wide as tergites (Figs 15, 16); tergite 1 fused to tergite 2; both sexes with tergites 2–5 (6) with transverse, submarginal sclerotised band (Fig. 15); tergites 2–7 in female and tergites 2–6 in male with long, thick posterolateral seta (sometimes reduced); sternites sometimes with smaller posterolateral seta; sternite 1 small, bare; spiracles in membrane below tergites 2–6; spiracle 7 absent; female abdomen past segment 7 short, often withdrawn; cerci separate (Figs 15, 16), sub-cylindrical or broad and plate-like; epiproct sometimes fused to tergite 8; spermatheca (1 pair) darkly pigmented, spherical (Fig. 17); sperm ducts (Fig. 17) widest apically (approximately ⅓–½ width of spermatheca), with apex sometimes pigmented; ventral receptacle (Fig. 17) simple, sub-cylindrical, narrowing apically; male abdomen (Figs 9–11) attaining symmetry secondarily in a few species; sternites 6–8 sometimes atrophied and bare; usually with sternite 6 separate, subrectangular, ventral to left lateral; sternite 7 smaller, subrectangular or band-like, left lateral and sometimes partially fused to sternite 8; sternite 8 dorsal and well-developed to band-like; right lateral supernumerary sclerite (homology uncertain) sometimes present; epandrium weakly sclerotised posteriorly, separate from, articulated to or partially fused to surstylus; sometimes with 1 or 2 pairs of large, stout setae; proctiger membranous, raised, sometimes with 1 pair of clear sclerotised ridges; cerci separate, pale and setulose, sometimes broad and plate-like; male terminalia with surstylus (Figs 10, 11) well-developed, setulose; (subepandrial sclerite) weak, band-like, removed from epandrium and associated with base of hypandrium; hypandrium (Figs 12, 13) broad and relatively flat, with 1 pair of short posterobasal "arms", sometimes with posteroventral margin produced into broad lobe (*Neurochaeta*), with 1–3 setae, articulating with or fused to pregonite(s) (Figs 12, 13); pregonite (Fig. 12) in 1–2 pairs, setulose; phallapodeme short and rod-like, sometimes lateral margins produced as plate fusing with inner medial margins of hypandrium (Fig. 13); basiphallus (Fig. 12) short, cylindrical, fused to distiphallus, sometimes striated/ridged; distiphallus (Fig. 12) long (sometimes exceeding length of abdomen), narrow and at least partially coiled, with 2 (*Neurotexis*) or more (*Neurocytta*) sclerotised bands along length, or membranous surface minutely textured and sometimes with lightly sclerotised line along length (*Neurochaeta*); ejaculatory apodeme (Fig. 14) with broad base on large clear basal bulb, stem stout, mostly confluent with ill-defined and relatively short blade.

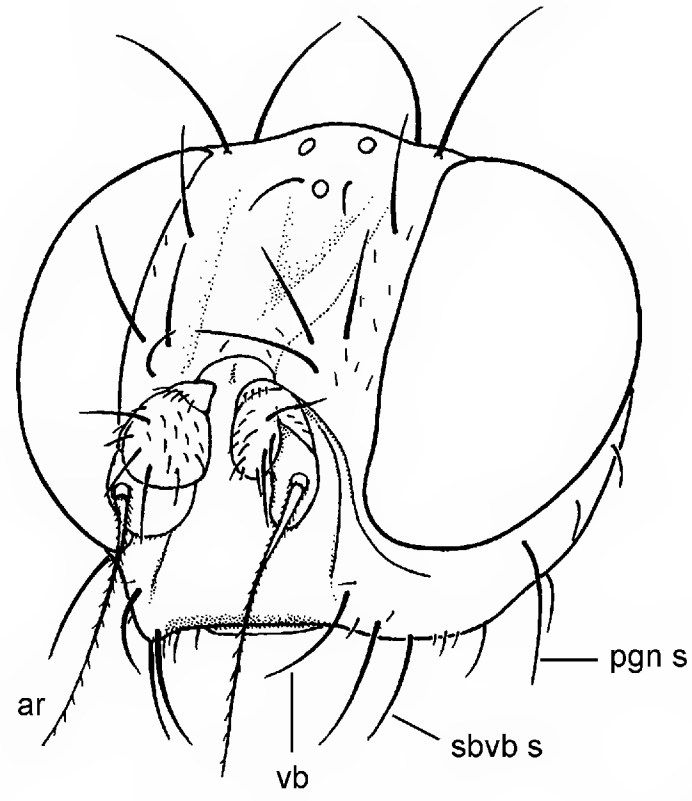
Descriptions of third-instar larva and puparia are available for *Neurochaeta inversa* in McAlpine (1978). Larva (Figs 18–22) colourless; typical of most other Acalyptratae; *ca* 4 mm in length, narrow and sub-cylindrical with segments evident and ends tapered (Fig. 18); mostly smooth, although segments with rows of spicules ventrally, which on abdominal segments 2–7 form 1 dominant pair of pad-like creeping welts with hooked spicules; abdominal segment 8 slender, narrowed medially, with 1 pair of elongate anal papillae flanking anus and medial subconical process bearing spiracles; oral opening of pseudocephalon flanked anteriorly by 3 small papillae and anterolaterally by rows of "rake-like" cirri (Fig. 19); posterior spiracles (Fig. 20) on short tubercles, each with 3 central spiracular openings in 1 row and 4 short, branched peristigmatic tufts; prothoracic spiracles (Fig. 21) each on short, narrow process with bulbous apex; 3 terminal papillae at end of short "urn-shaped" extension; cephaloskeleton (Fig. 22) weakly pigmented, with elongate parastomal bar, dark pigmentation along anterior margin of anterior sinus, dorsal cornu slender and floor of ventral cornu with cibarial ridges.

Puparium (Fig. 23) curved and spindle-shaped, with ends strongly tapered; smooth, shiny, yellowish and translucent, with minute reticulate pattern partially visible; most segments with 3 annular thickenings that form ridges along inner surface.

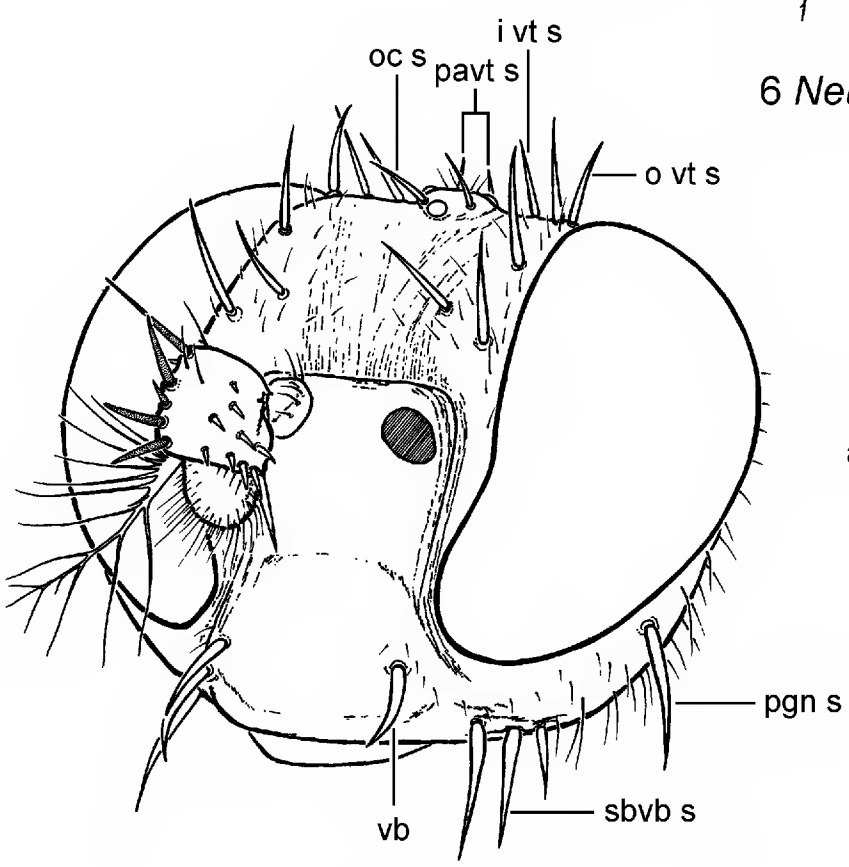
Among the Acalyptratae, adult Neurochaetidae are most similar in appearance to the Periscelididae (see Chapter 91), with which they share reclinate and proclinate fronto-orbital setae and a similarly enlarged, cap-like antennal pedicel. Most Neurochaetidae also have a bipectinate arista and some *Neurotexis* have the venter of the face angled downwards (Fig. 8). Neurochaetids differ in often being conspicuously flattened on the thorax, having more than two fronto-orbital setae, a single costal wing break, distinct spinules along the costal vein (most species), abdominal sternites virtually as broad as the tergites and unusually proportioned legs (mid leg reduced, hind leg enlarged and hind and sometimes fore femur relatively stout).

Biology and immature stages

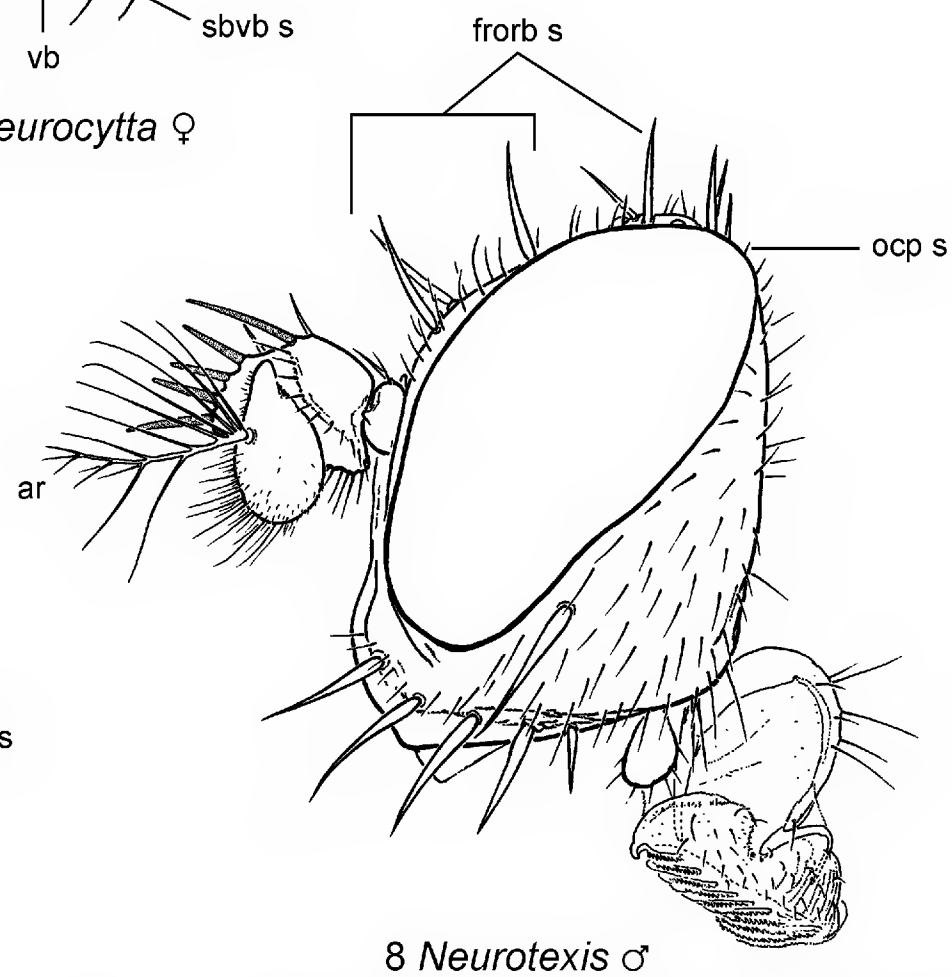
The most obvious behavioural characteristic of Neurochaetidae is the head down orientation of the adult on vertical or steep surfaces (Fig. 1), hence their vernacular name "upside-down flies". Specimens of all extant genera have been observed running rapidly on plant surfaces in a zigzag motion, both forwards and backwards, but almost invariably maintaining a head down orientation (McAlpine 1978, 1988*a*, 1993, 2011). Head up orientation was sometimes observed if flies were injured, or if they ran to the end of a drooping leaf (McAlpine 2011).



6 *Neurocytta* ♀



7 *Neurotexis* ♂



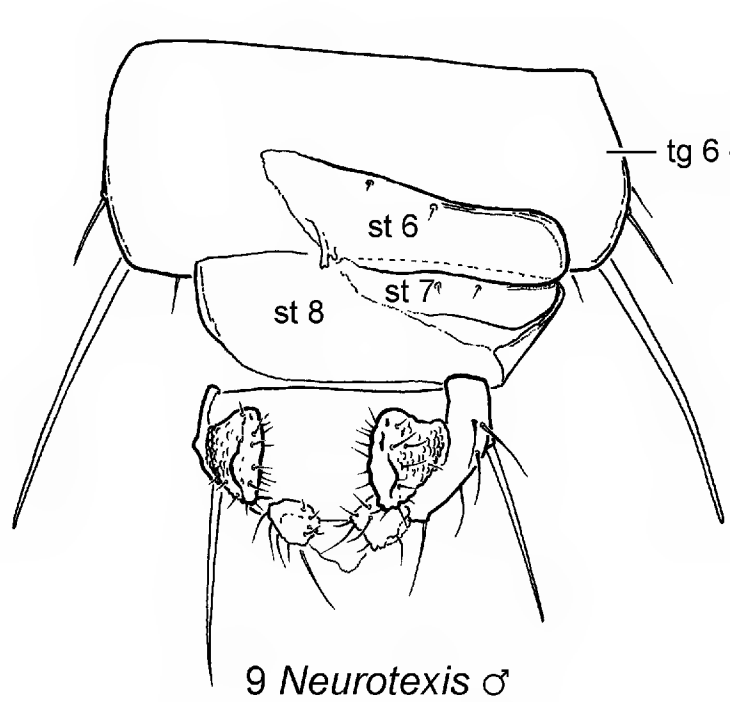
8 *Neurotexis* ♂

Figs 90.6–8. Heads of Neurochaetidae: (6) *Neurocytta prisca* McAlpine, anterolateral view ♀; (7) *Neurotexis charis* McAlpine, anterolateral view ♂; (8) same, lateral view. Fig. 6 (McAlpine 1993, fig. 1A).

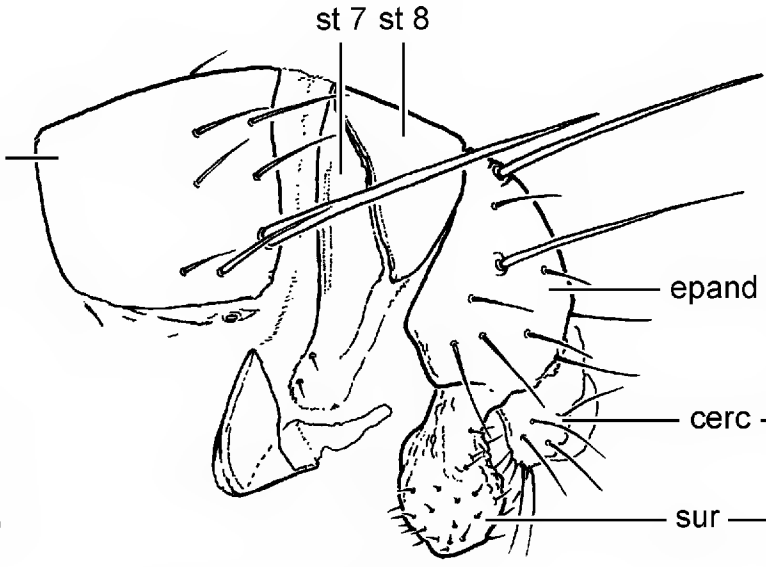
Abbreviations: ar – arista; frorb s – fronto-orbital seta; i vt s – inner vertical seta; o vt s – outer vertical seta; oc s – ocellar seta; ocp s – occipital seta; pavt s – paravertical seta; pgn s – postgenal seta; sbvb s – subvibrissal seta; vb – vibrissa.

Species occur in wet habitats, especially rainforests and appear to be closely associated with particular monocotyledonous host-plants, within which the larvae feed and on which adults occur. Humid environments near leaf bases and sometimes other crevices in plants, often containing pools of water, appear to be most favourable (McAlpine 1978, 1988*b*, 2011). A list of observed and putative host-plant associations is provided by McAlpine (1993). The biology of the Australian species, *Neurochaeta inversa* McAlpine, 1978, was originally described in McAlpine (1978) and later much elaborated upon in McAlpine (1988*b*), detailing activities of the fly on *Alocasia* (Araceae). Larval feeding habits are unknown, but no visible damage has been observed on host-plants and it is hypothesised that the nutritive source is liquid-suspended micro-organisms in the enclosed spathal chamber that seals following fertilisation. As the host fruit matures, the yellowed spathe withers and unfurls, allowing the eclosed adults to escape. Adults emerge through openings formed in the chamber, even tiny cracks, facilitated by their dorsoventrally compressed body (McAlpine 1978). Larval stages are only known to occur within the host-plant, with adults representing the overwintering phase, suggesting that multiple generations may exist if they coincide with flowering and fruiting of the host (McAlpine 1978).

Adult feeding is known for *Neurochaeta inversa* (McAlpine 1988), with specimens observed ingesting pollen from the host-plant and the pollen load of a bee at the host; adults have also fed on drops of diluted jam smeared on host-plant leaves,

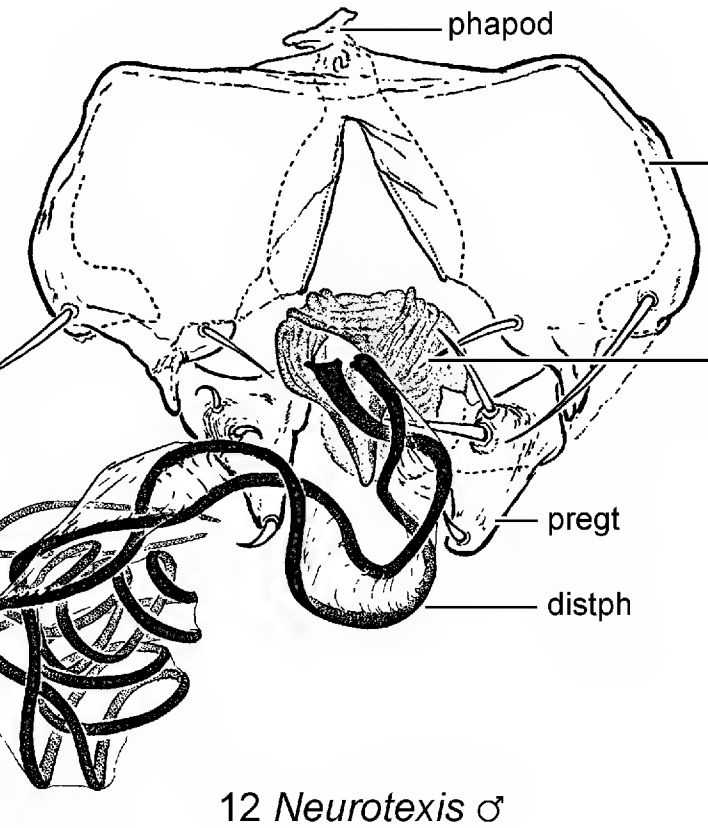


9 *Neurotexis* ♂

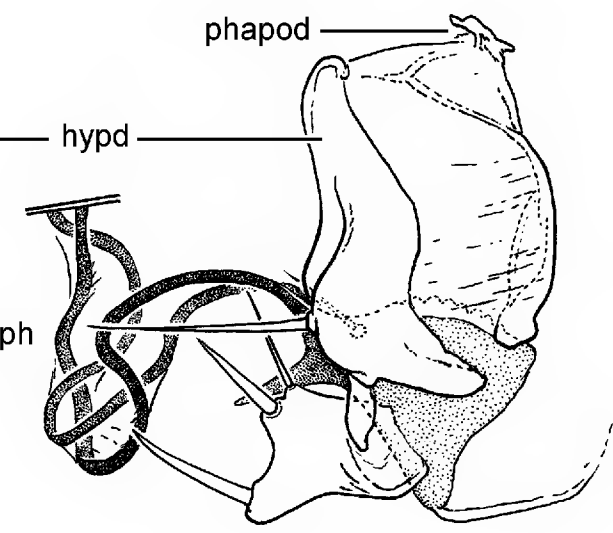


10 *Neurotexis* ♂

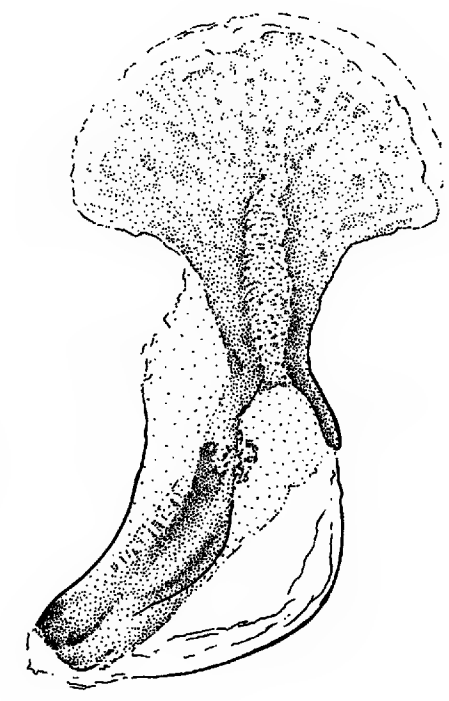
11 *Neurotexis* ♂



12 *Neurotexis* ♂



13 *Neurotexis* ♂



14 *Neurotexis* ♂

Figs 90.9–14. Male terminalia of Neurochaetidae: (9) external components of *Neurotexis charis* McAlpine, ventral view; (10) same, lateral view; (11) same, posterior view; (12) same, internal components, ventral view; (13) same, lateral view; (14) same, ejaculatory apodeme, lateral view.

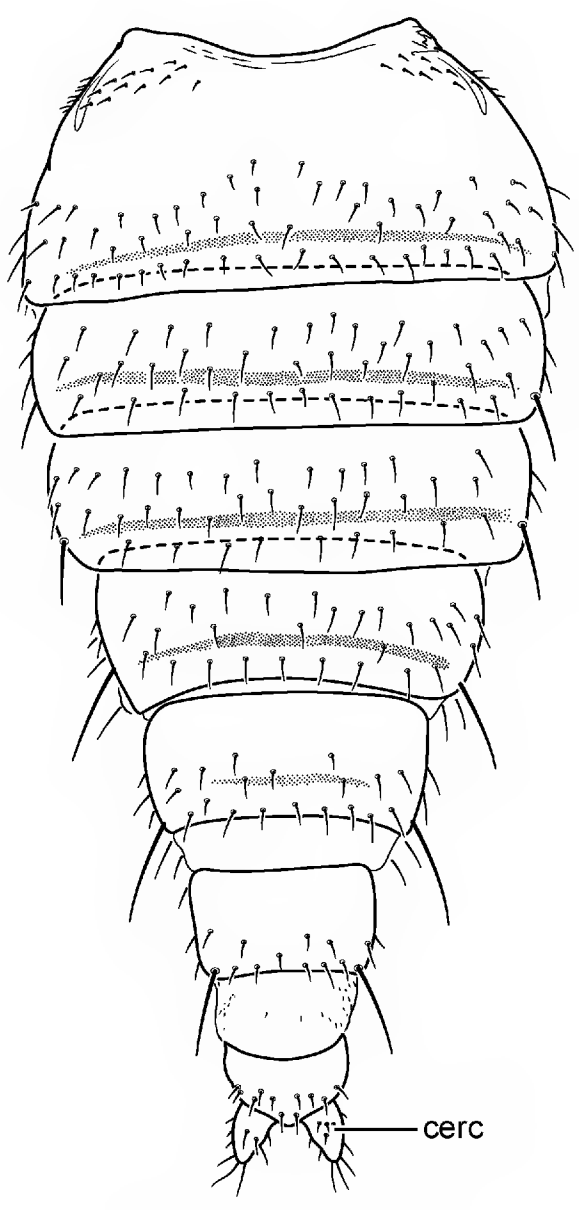
Abbreviations: basph – basiphallus; cerc – cercus; distph – distiphallus; epand – epandrium; hypd – hypandrium; phapod – phallapodeme; pregt – pregonite; st – sternite; sur – surstylus; tg – tergite.

supporting McAlpine's (1988*b*) hypothesis that food substances accumulating on these leaves support flies when the host is not in flower.

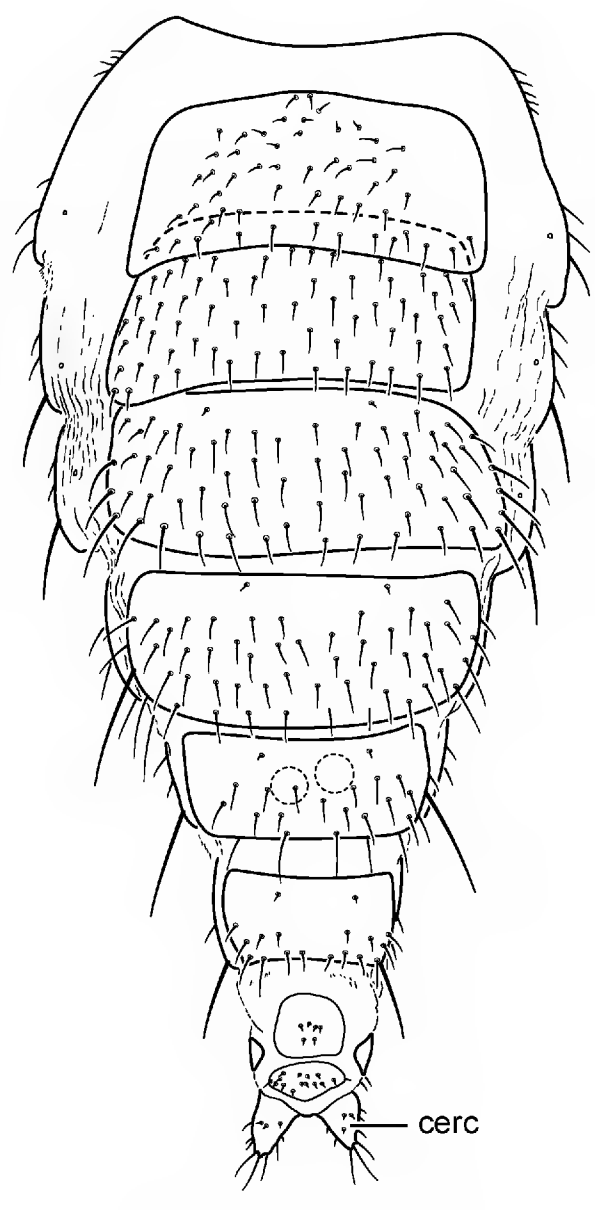
Shaw *et al*. (1982) expanded on McAlpine's studies, examining fly abundance and distribution on *Alocasia brisbanensis* (F.M. Bailey) Domin (originally determined as *A. macrorrhiza* (L.)) in varied environments and their effect on seed production. They confirmed that adult eclosion was timed to occurrence of infructescence maturation, specifically, during the period of deliquescence of the host florets. Larvae were recovered on the inner surface of the spathal tube, in a broth at the bottom of the spathal chamber produced from deliquescence of the host florets and on the outer surface of berries and unfertilised ovaries. Development of larvae was not entirely synchronised within a single plant, with larvae and puparia sometimes recovered simultaneously. Pupariation was completed for all larvae upon disappearance of the broth and floret remains, with individuals positioned between berries. Host seed production was not affected by population size of the flies, which are likely not the only pollinators.

Woodley (1982) further described *Neurochaeta macalpinei* from adults taken from *Alocasia macrorrhiza* in Malaysia and McAlpine (1988*b*) added additional detail on life history for the Malaysian fauna, although only adults were observed and host associations are yet to be substantiated. *Neurochaeta magnifica* McAlpine, 1988 was noted to occur on upright *Pandanus* L. (Pandanaceae) leaves, *N. capilo* McAlpine, 1988, was observed on petioles of wild banana, *Musa* sp. (Musaceae) and *N. parviceps* McAlpine, 1988 (mostly males) was found on young inflorescences of wild ginger, *Zingiber spectabile* Griff (Zingiberaceae). All potential hosts provide phytotelmata, within which larvae could potentially feed and develop. The adult Malaysian specimens moved similarly to *N. inversa* and individuals often ran, but sometimes flew when disturbed, only leaving the presumed host-plant after some disturbance. More recently, the Australian *Nothoasteia clausa* McAlpine, 1988, was collected in significant numbers in the crown of Balga, *Xanthorrhoea preissii* Endlicher (Xanthorrhoeaceae) (McAlpine 2011); this observation may be indicative of the occurrence of many other neurochaetid species considered uncommon or rare, being instead relatively abundant and widespread in association with their host-plants.

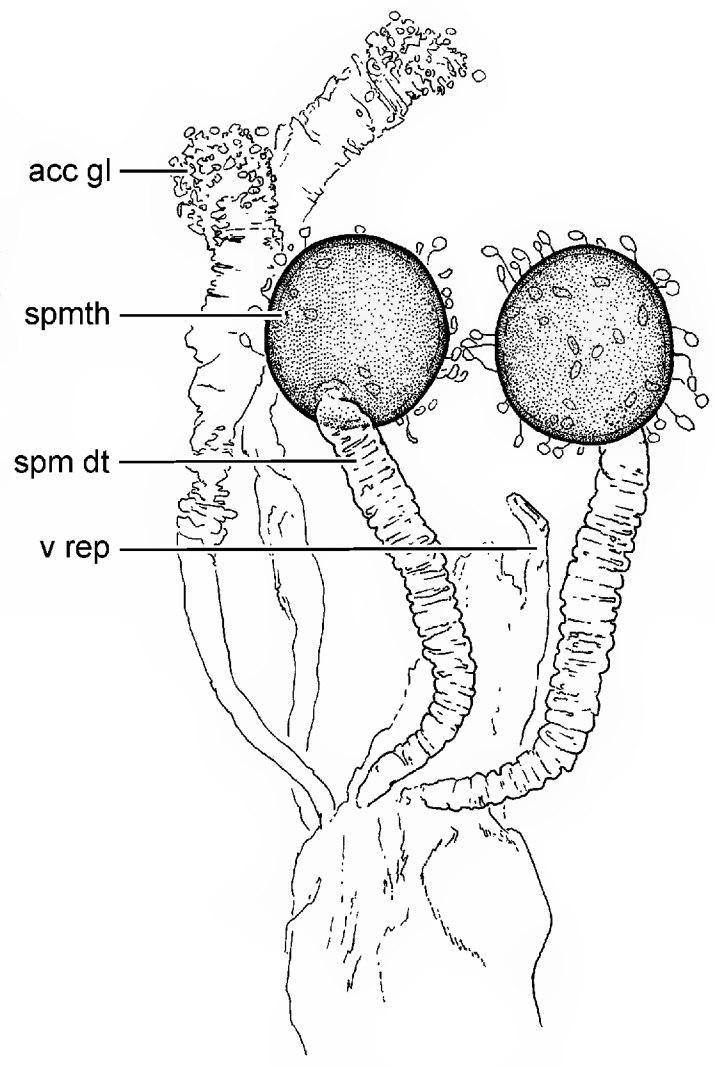
In the Afrotropical Region, McAlpine (1993) suggested that the distribution of *Neurocytta prisca* McAlpine, 1978, was limited to that of plants of the genus *Strelitzia* (Strelitziaceae),



15 *Neurotexis* ♀



16 *Neurotexis* ♀



17 *Neurotexis* ♀

Figs 90.15–17. Female abdomens and internal female terminalia of Neurochaetidae: (15) abdomen of *Neurotexis charis* McAlpine, dorsal view; (16) same, ventral view; (17) same, internal terminalia.

Abbreviations: acc gl – accessory gland; cerc – cercus; spm dt – sperm duct; spmth – spermatheca; v rep – ventral receptacle;

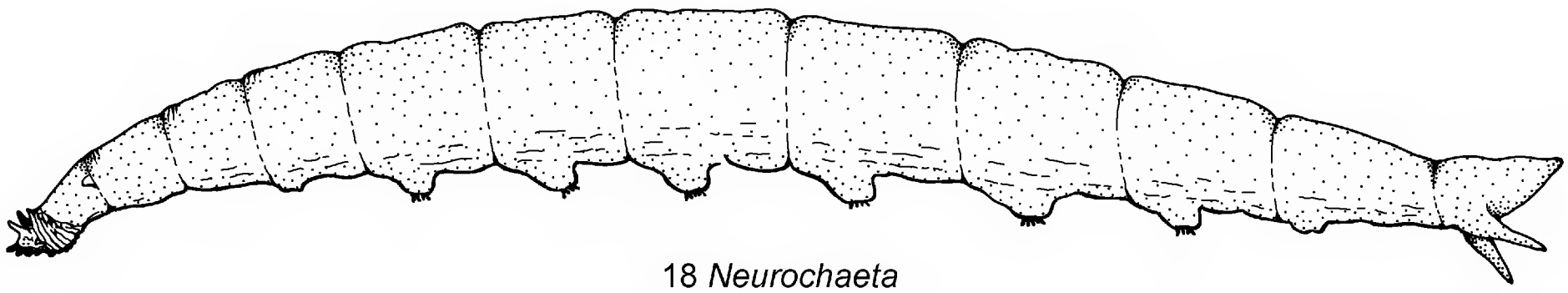
due to his observations of adults – including some that were newly eclosed – on leaves and lateral branches near the plant base. Species of *Neurotexis* are associated with *Pandanus* and *Ravenala* (Strelitziaceae), although these observations are also restricted to adults (McAlpine 1993).

Economic significance

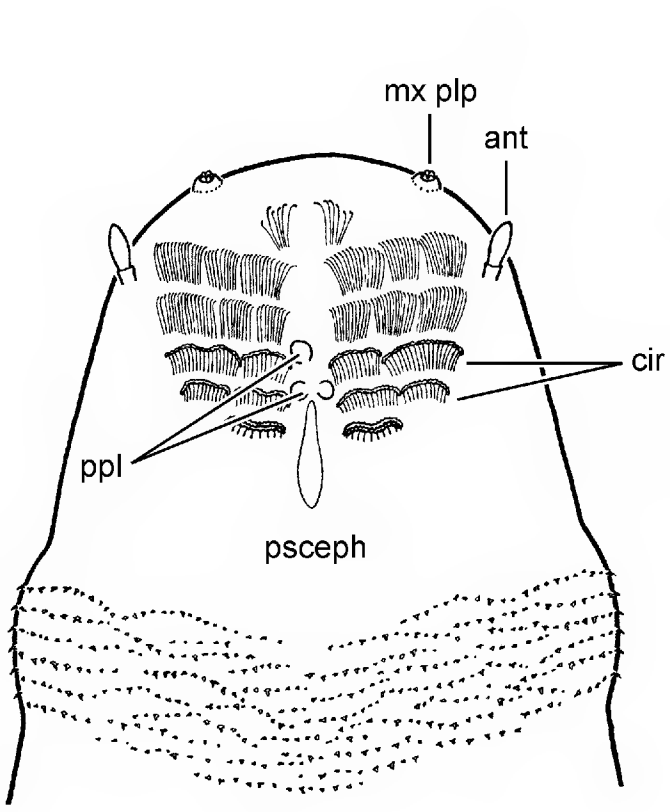
No species of economic significance are currently known.

Classification

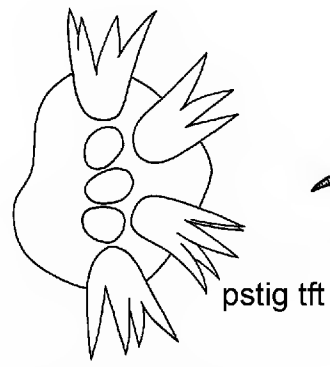
Neurochaeta was described by McAlpine (1978) as the type genus for his new family Neurochaetidae, which at the time included three newly described extant species from Australia, Madagascar and Zimbabwe. The two Afrotropical species were catalogued by Cogan (1980: 653). McAlpine's (1978) new family also included two fossil species of *Anthoclusia* Hennig from Baltic amber dating to the Oligocene (33.9–23 MYA), previously described by Hennig (1965, 1969) as Anthomyzidae. Later, Hennig (1971) re-evaluated his original family-level placement of the fossils, leaving *Anthoclusia* unplaced in his division Periscelidea, superfamily Anthomyzoidea. McAlpine (1978) placed the Neurochaetidae in his superfamily Asteioidea, which he considered to be nearly equivalent to Hennig's Periscelidea. The superfamily Asteioidea was later repurposed by McAlpine (1989: 1462) as the suprafamily Asteioinea in his superfamily Opomyzoidea, where the Neurochaetidae currently resides. A study by Winkler *et al*. (2010), however, strongly suggests that hypothesised relationships among the



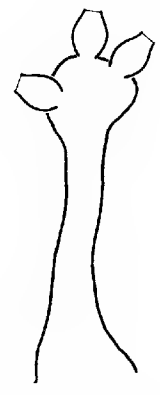
18 *Neurochaeta*



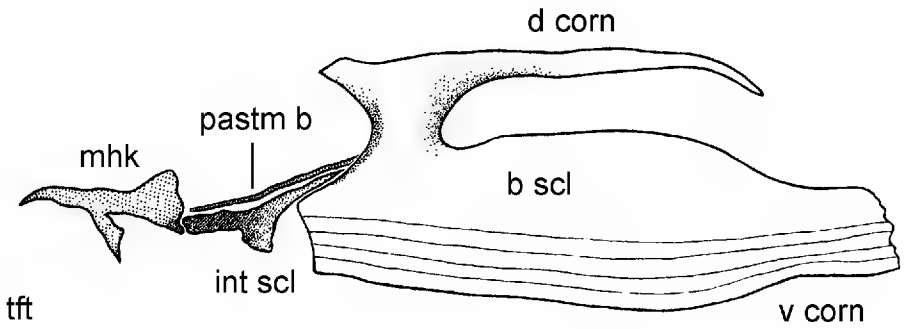
19 *Neurochaeta*



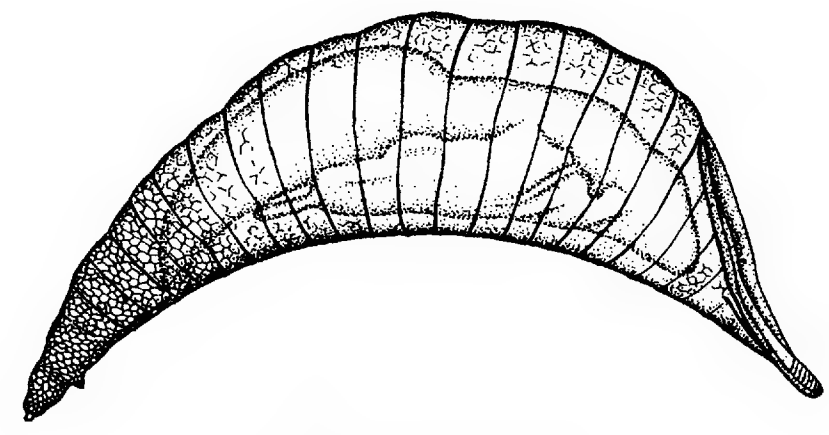
20 *Neurochaeta*



21 *Neurochaeta*



22 *Neurochaeta*



23 *Neurochaeta*

Figs 90.18–23. Immature stages of Neurochaetidae: (18) habitus of third-instar larva of *Neurochaeta inversa* McAlpine, lateral view (non-Afrotropical); (19) same, anteroventral region, ventral view; (20) same, posterior spiracle, dorsal view; (21) same, prothoracic spiracle, dorsal view; (22) same, cephaloskeleton, lateral view; (23) same, puparium, lateral view. Figs 18–23 (McAlpine 1978, figs 4, 24, 22, 23, 13, 25, respectively).

Abbreviations: ant – antenna; b scl – basal sclerite; cir – cirri; d corn – dorsal cornu; int scl – intermediate sclerite; mhk – mouthhook; mx plp – maxillary palpus; ppl – papillae; pastm b – parastomal bar; psceph – pseudocephalon; pstig tft – peristigmatic tuft; v corn – ventral cornu.

families of the Opomyzoidea, including those in the supra-family Asteioinea, are likely artificial, being largely unsupported in their molecular analyses.

Within the Neurochaetidae, Woodley (1982) described two new species from South-east Asia and proposed the first phylogeny of *Neurochaeta*. This phylogeny supported *N. prisca* as sister to the remaining species in the genus, and *N. stuckenbergi* McAlpine, 1978 as sister to the "*N. inversa*-group", which contained the remaining Asian and Australian species. Woodley (1982) noted that these three lineages of *Neurochaeta* might eventually warrant genus-level ranking, which was later pursued by McAlpine, who first treated them as subgenera (McAlpine 1988*a*) and then finally providing them with full generic rank (McAlpine 1993).

McAlpine (1988*a*) placed *Neurochaeta prisca* (Zimbabwe) in the monotypic *Neurocytta* and placed *Neurochaeta stuckenbergi* (Madagascar) in the monotypic *Neurotexis* (Figs 2–4), which was later expanded to include ten additional species (McAlpine 1993). The Australasian species of Woodley's (1982) "*N. inversa*-group" were treated as *Neurochaeta sensu stricto*. Unlike the above Afrotropical genera, *Neurochaeta sensu stricto* is partially characterised by dorsal setulae basally on veins R_1 and R_{4+5} (*Neurocytta prisca* with a few small setulae on vein R_1), additional marginal setae on the scutellum, reduction to absence of the anterior dorsocentral seta and usually plate-like female cerci. As well as describing an additional three species in *Neurochaeta* and subdividing it into several species-groups, McAlpine (1988*a*) also expanded the Neurochaetidae to include the Australasian genus *Nothoasteia*. Previously considered Asteiidae, *Nothoasteia* is characterised by setulose eyes, an absence of the alular fringe, a complete costal vein (*C*) and severe reduction and modification of the tarsal claws into thin, plumose processes (McAlpine 2011, fig. 7).

Identification

The family Neurochaetidae currently consists of the fossil genus *Anthoclusia* (two species; type species: *A. gephyrea* Hennig, 1965) and four extant genera: *Neurochaeta* (six species; type species: *N. inversa*); *Neurocytta* (one species; type species: *N. prisca*); *Neurotexis* (11 species; type species: *N. stuckenbergi*); and *Nothoasteia* (two species; type species: *N. platycephala* Malloch, 1936). Two genera of Neurochaetidae occur in the Afrotropical Region: *Neurocytta* (Zimbabwe) and *Neurotexis* (Madagascar). Neurochaetidae are best micropinned in the field for later double-mounting (see Chapter 2).

Key to genera of Afrotropical Neurochaetidae

1. Antennal arista short plumose (Fig. 6); thorax with 2 katepisternal setae; subscutellum small, undeveloped, microtrichose; apical scutellar setae closely spaced; wing with subcostal break simple; costal vein (C) extending to vein M_1; vein R_1 with a few weak dorsal setulae (Zimbabwe) . . . . *Neurocytta* McAlpine

– Antennal arista bipectinate (Figs 7, 8); thorax often with 1 katepisternal seta, sometimes with second weak to well-developed seta present; subscutellum large, prominent, tomentose (Fig. 2); apical scutellar setae widely spaced, approximately as close to each other as to lateral corner of scutellum; wing with costal vein (*C*) extending to vein R_{4+5}, usually produced into a lappet at subcostal break (Figs 4, 5); vein R_1 bare (Madagascar) . . . . . *Neurotexis* McAlpine

Synopsis of fauna

***Neurocytta* McAlpine.** An endemic monotypic genus, with the single species, *N. prisca* (Fig. 6), known from a limited area in Zimbabwe (Chimanimani, as "Melsetter"). The genus is characterised by two katepisternal setae, a short plumose arista, a closed basal medial wing cell (*bm*) and a few weak dorsal setulae on vein R_1. The wing, scutellum and male terminalia were figured by McAlpine (1978, figs 9, 11, 21). The species is probably associated with plants of the genus *Strelitzia* (Strelitziaceae) (McAlpine 1993).

***Neurotexis* McAlpine.** An endemic genus confined to Madagascar and revised by McAlpine (1993), now comprising 11 species. Unlike *Neurocytta*, but similar to the non-Afrotropical *Neurochaeta*, *Neurotexis* has a bipectinate arista, a prominent subscutellum, widely spaced apical scutellar setae and often atrophy of crossvein *bm–m*. *Neurotexis* is further characterised by termination of the costal vein at vein R_{4+5}, a costal vein produced into a lappet at the subcostal break, an atrophied/spectral ultimate section of vein M_1 and the presence of presutural setae. An identification key to species was provided by McAlpine (1993), but additional species from Madagascar await description.

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PERISCELIDIDAE 91

(Dwarf Flies)

Alessandra Rung and Wayne N. Mathis

Fig. 91.1. Male (right) and female (left) of *Stenomicra* sp. (Madagascar) (photograph: © S.A. Marshall).

Diagnosis

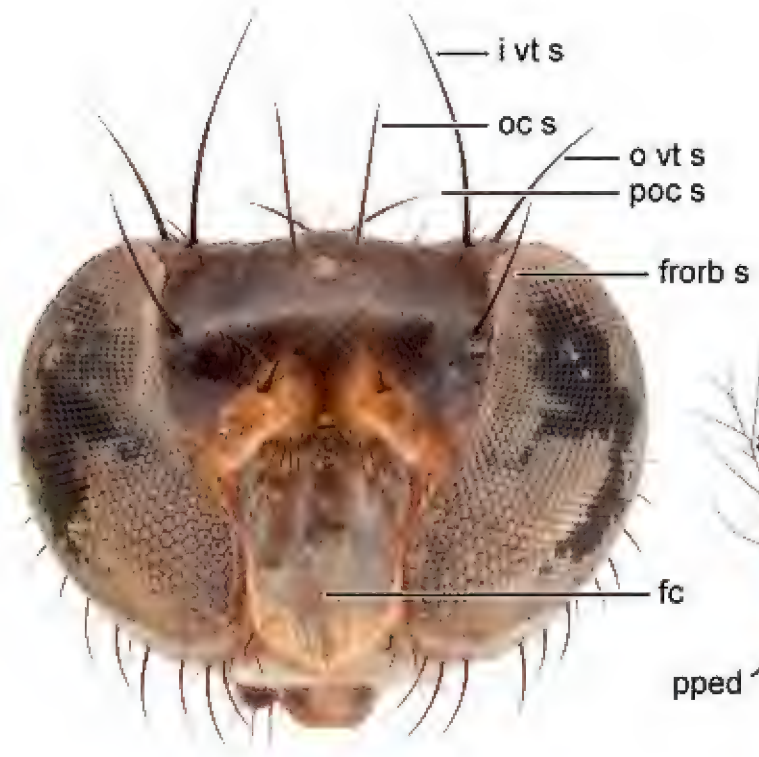
Moderately small- to medium-sized acalyptrate flies (body length: 2.5–5.0 mm), broad to slender (Fig. 1); colouration mainly dark brown to black (species in all genera), or yellow, with or without brown patterns (some *Stenomicra* Coquillett); wing entirely hyaline, or partly infuscate with brown.

Head (Figs 2–4, 12, 13) with face uniformly sclerotised, protruding, ventral portion receded; antenna with pedicel swollen and cap-like, with dorsal cleft, bearing 1–2 dorsoapical setae; postpedicel moderately to sharply deflexed, arising from ventral surface of pedicel (Fig. 3); arista with dorsal and ventral branches; ocellar seta (when present), inserted laterally to margin of ocellar tubercle; inner vertical seta generally present (absent in *Cyamops* Melander); postocellar seta, when present, reduced, divergent; 1–2 fronto-orbital setae present, with 1 seta reclinate; interfrontal seta generally absent (present, dorsoclinate and slightly reclinate in the Neotropical genus *Planinasus* Cresson).

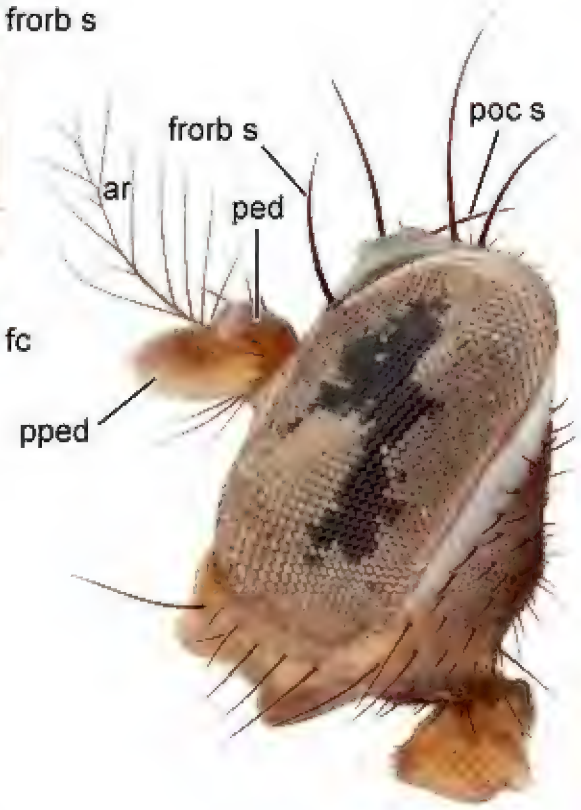
Thorax (Fig. 5) with dorsocentral setae 0 + 1 or 0 + 2; posterior intra-alar seta reduced; 1–2 pairs of scutellar setae; disc of scutellum bare. Wing (Figs 8–11) without true costal breaks; subcostal vein (*Sc*) incomplete, not fused with vein R_1 apically; costal vein (*C*) extended to vein R_{4+5}, or vein M_1; cell *dm* with longitudinal fold (fold inconspicuous in some *Stenomicra*); cell *cua* typically present, although *CuA* either well-developed or reduced.

Male preabdomen (Figs 6, 7, 17) consisting of 6 segments, with postabdomen either symmetrical (Fig. 7), or asymmetrical (Fig. 17); male terminalia with surstylus discrete, articulated (Figs 16, 17) or fused with epandrium (Figs 7, 14); cercus

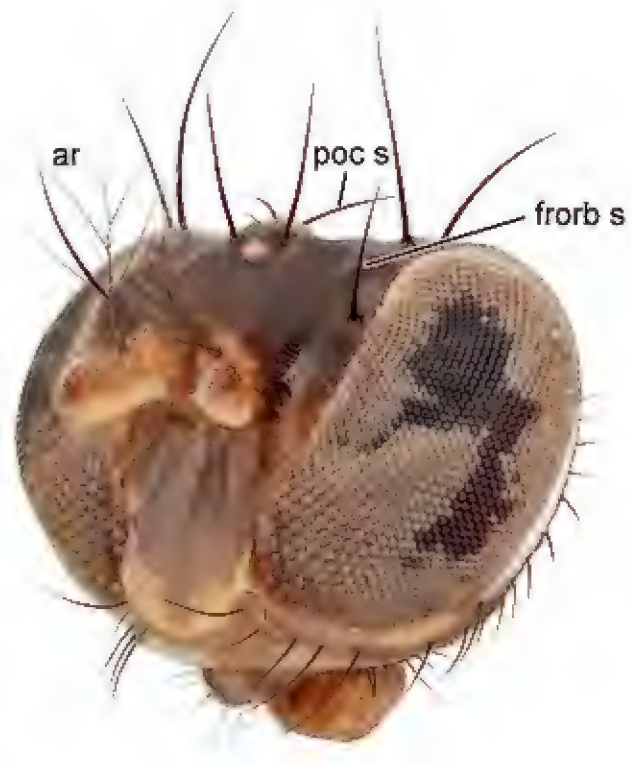
Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2021. Manual of Afrotropical Diptera. Volume 3. Brachycera—Cyclorrhapha, excluding Calyptratae. *Suricata* 8. South African National Biodiversity Institute, Pretoria; pp. 1981–1987.



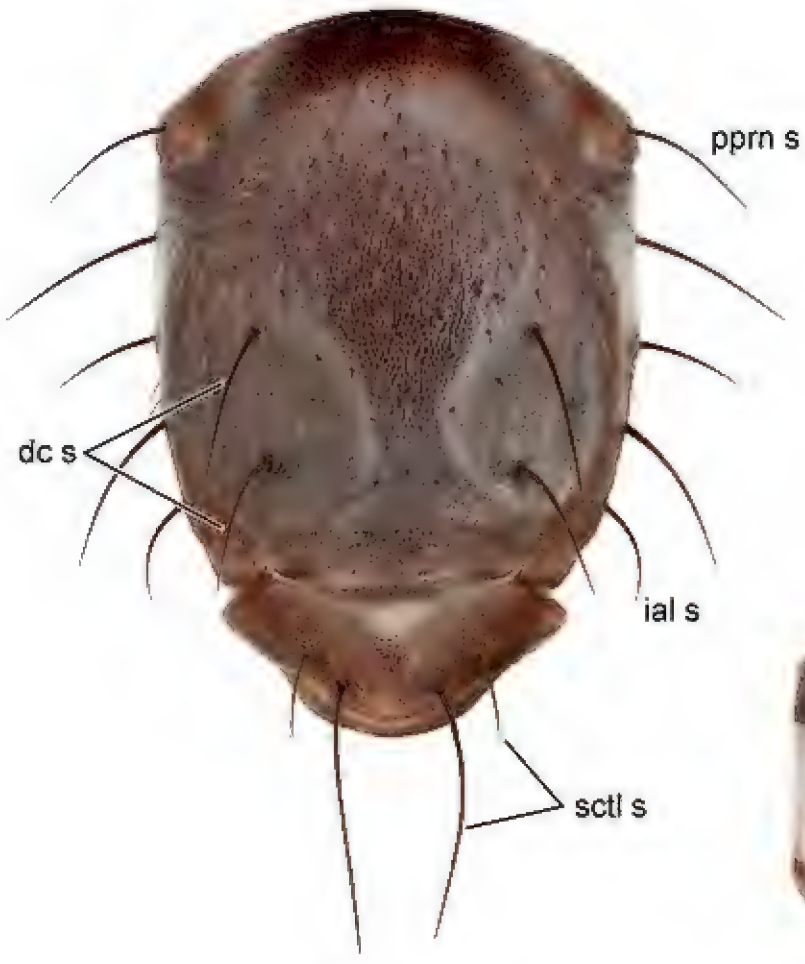
2 *Periscelis*



3 *Periscelis*



4 *Periscelis*



5 *Periscelis*

6 *Periscelis* ♂

7 *Periscelis* ♂

Figs 91.2–7. Heads, mesonotum and abdomens of Periscelididae: (2) head of *Periscelis stuckenbergi* Mathis & Freidberg, anterior view; (3) same, lateral view; (4) same, frontolateral view; (5) same, mesonotum, dorsal view; (6) male abdomen of *P. occidentalis* Sturtevant (non-Afrotropical), dorsal view; (7) same, lateral view. Figs 2–5 (Mathis & Freidberg 2012, figs 1, 2, 3, 5).

Abbreviations: ar – arista; cerc – cercus; dc s – dorsocentral setae; epand – epandrium; fc – face; frorb s – fronto-orbital seta; i vt s – inner vertical seta; ial s – intra-alar seta; o vt s – outer vertical seta; oc s – ocellar seta; ped – pedicel; poc s – postocellar seta; pped – postpedicel; pprn s – postpronotal seta; sctl s – scutellar setae; sur – surstylus; tg – tergite.

strongly or weakly sclerotised; hypandrium strongly modified in Periscelidinae, more or less fused with phallapodeme, forming a bursa-like hypandrial complex (Fig. 14) where the "... aedeagus is folded when at rest" (Griffiths 1972: 121), strongly asymmetrical in *Cyamops* (Fig. 16), posteriorly open, anteriorly with or without hypandrial bridge connecting phallapodeme; gonopods forming a complex with hypandrium; phallus variable, ribbon-like in *Periscelis* Loew (Fig. 14), membranous to strongly sclerotised and complex in *Cyamops* (Fig. 16) and *Stenomicra*; female abdomen (Fig. 18) with tergite and sternite 6 separate, or fused to each other, forming complete ring (*Cyamops*) (Fig. 18); with tergite and sternite 7 separate, or fused to each other, forming complete ring or with tergite 7 weakly sclerotised (Fig. 18); 2–4 spermathecae present.

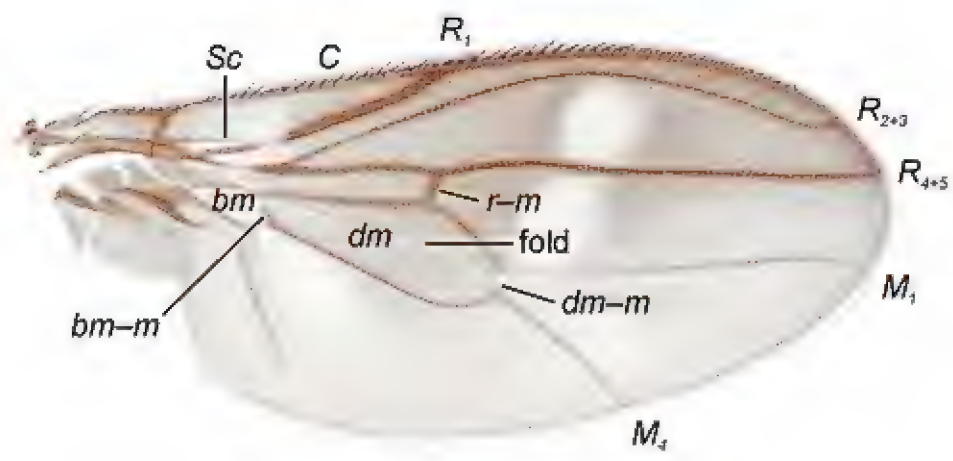
Egg (based on three European species of *Periscelis*) (Fig. 19), blue (sky blue to violet); boat-shaped, long ovoid in dorsal view, without filaments; ventral portion convex, lighter in colour than dorsum, with fine, irregular, hexagonal network; dorsal portion darker, less convex, but not flat, with 2 fine ribs confluent at apices, lacking network but micro-sculptured; micropyle inconspicuous.

Papp (1995) summarised larval features of *Periscelis* (subgenera *Periscelis* and *Myodris* Lioy) as follows (Figs 20–22): larva with body strongly flattened dorsoventrally; segments with fleshy digitiform processes laterally and several other bulbous processes, all processes with large, partly curved spicules; subanal pads indistinct (with bifid inflated protuberance that can be extroverted from anus in *P. annulata* (Fallén, 1813)); prothoracic spiracle short, bulbiform, with 4–5 small bulbous papillae (Fig. 21); posterior spiracles (with peristigmatic tufts) on pair of long divergent spiracular processes (Fig. 20); cephaloskeleton (Fig. 22) with robust body (basal sclerite); mouthhooks strong, composed of curved apical part and robust basal (posterior) part and with 1 pair of ventrobasal, midventral and dorsal processes each; extremely long and thin parastomal bar; dental sclerite well-sclerotised (Papp 1995, fig. 3); basal sclerite with dorsal cornu much shorter than ventral cornu; ventral cornu robust. Larvae of *Myodris* plump, those of *P.* (*Periscelis*) slim; lateral process of posterior spiracular process distal to middle in *Myodris*, or proximal in *Periscelis* (extended to middle of posterior spiracle) (Mathis & Papp 1998).

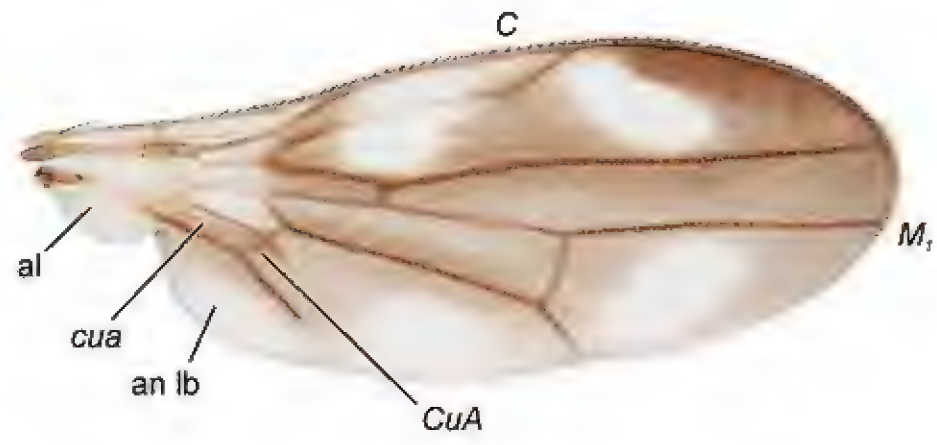
Adult periscelidids are readily distinguished from Aulacigastridae (see Chapter 88) and Anthomyzidae (see Chapter 87) genera by the shape of the pedicel, which is cap-like (Figs 3, 4); by the arista, which bears dorsal and ventral branches (Fig. 3); and by the longitudinal fold in wing cell *dm* (Fig. 8).

Biology and immature stages

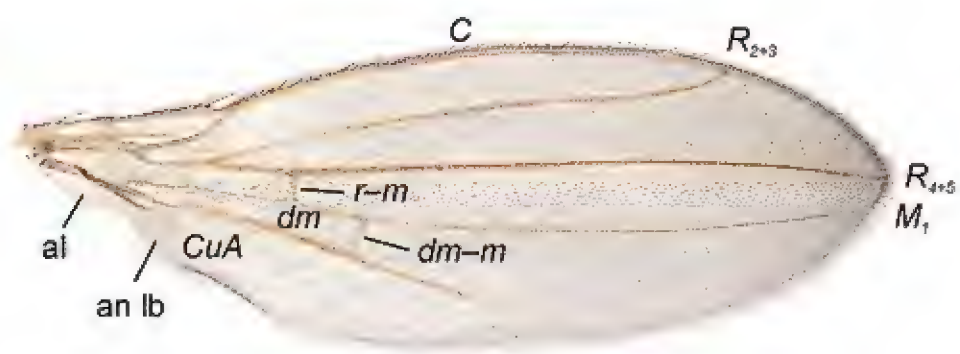
The immature stages of *Periscelis*, and to some extent the adults, are associated with oozing sap of deciduous trees (oak, elm, cottonwood, *etc.*). Papp (1998) described the habits and



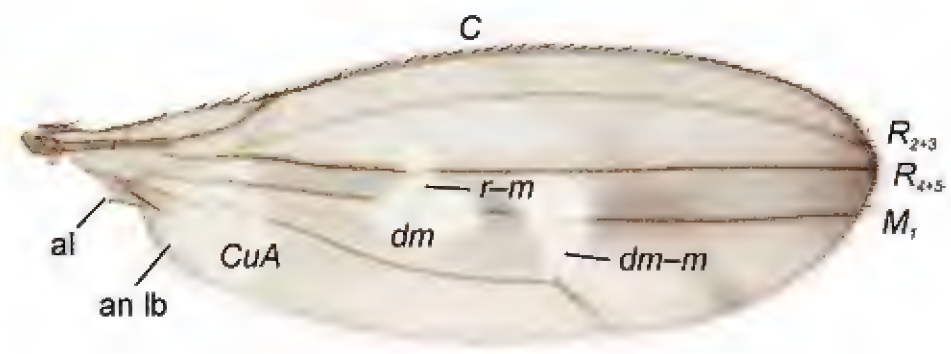
8 *Periscelis*



9 *Cyamops*



10 *Stenomicra* (*Stenomicra*)



11 *Stenomicra* (*Podocera*)

Figs 91.8–11. Wings of Periscelididae (dorsal views): (8) *Periscelis stuckenbergi* Mathis & Freidberg; (9) *Cyamops nigeriensis* Baptista & Mathis; (10) *Stenomicra* (*Stenomicra*) sp.; (11) *S.* (*Podocera*) *trimaculata* Sabrosky. Fig. 8 (Mathis & Friedberg 2012, fig. 4).

Abbreviations: al – alula; an lb – anal lobe; *bm* – basal medial cell; *bm–m* – basal–medial crossvein; *C* – costal vein; *CuA* – anterior branch of cubital vein; *cua* – anterior cubital cell; *dm* – discal medial cell; *dm–m* – discal medial crossvein; M_1 – first branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Sc* – subcostal vein.

habitats of three European species of *Periscelis*. Williams (1939) reported larvae of *Stenomicra* (*Stenomicra*) *orientalis* Malloch, 1927, at the water-holding leaf bases of several monocotyledons in Hawaii, including pineapple, *Ananas sativus* Schultes (Bromeliaceae) and some Liliaceae and Poaceae.

In the New World, *Stenomicra* larvae have been found in aquatic and semi-aquatic habitats of phytotelmata in Apiaceae (*Eryngium*), Araceae (*Xanthosoma*), Bromeliaceae and Poaceae (*Coik lacrymajobi* L. and *Pandanus*) (Campos *et al*. 2010: 110). A brief description of the life-cycle of an unidentified *Stenomicra* species can be found in Campos *et al*. (2010).

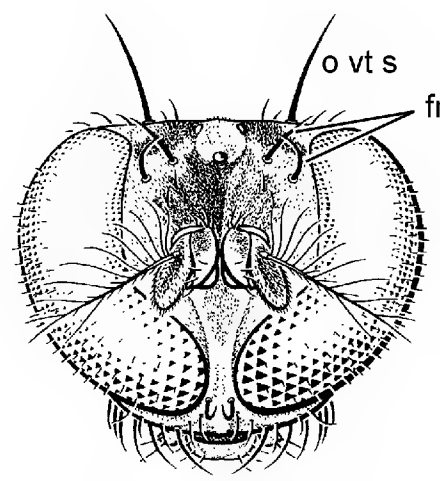
Economic significance

The Periscelididae have no economic importance. There are no records involving any species in agricultural, medical, veterinary or forensic works.

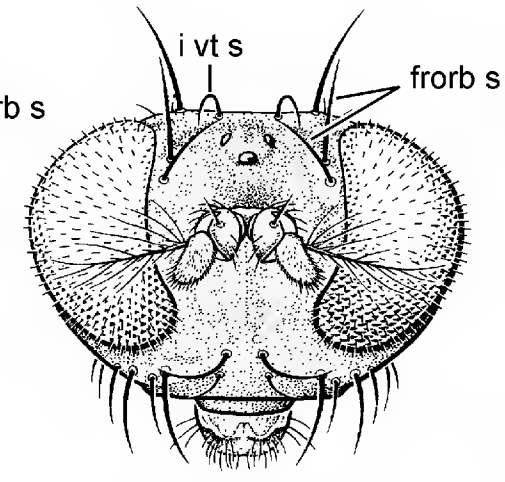
Classification

Periscelididae belong to the superfamily Opomyzoidea (McAlpine 1989: 1454) and the family's sister-group, according to McAlpine's phylogeny (1989: 1455), is the family Aulacigastridae. The concept of Periscelididae as adopted here follows McAlpine (1978, 1983) and includes a few genera previously assigned to Aulacigastridae (*Cyamops*, *Planinasus* and *Stenomicra*). McAlpine (1978, 1983) characterised Periscelididae primarily by the cap-like antennal pedicel, which has a dorsal cleft and its relationship to the postpedicel (geniculate; Fig. 3). Although these characters are common to all Periscelididae, they also occur in Neurochaetidae (see Chapter 90) (McAlpine 1978; Woodley 1982), a putative sister-group to the Periscelididae, according to Grimaldi & Mathis (1993) and in other acalyptrate families.

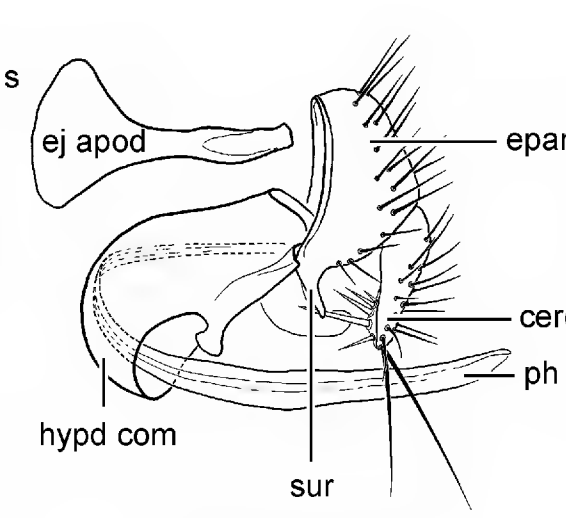
In a phylogenetic study of the Opomyzoidea, using 28S ribosomal DNA and CAD (rudimentary) genes (Winkler *et al*.



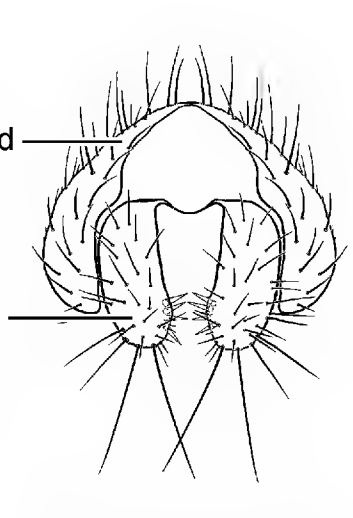
12 *Cyamops*



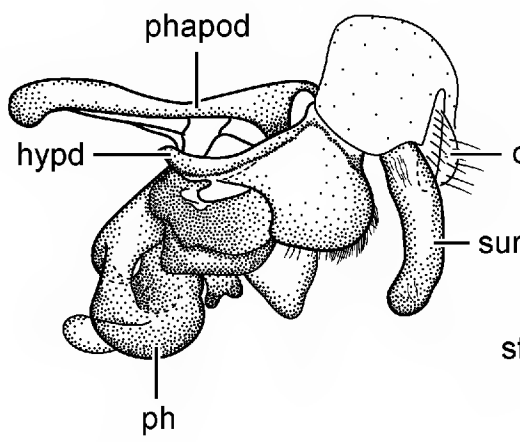
13 *Stenomicra* (*Stenomicra*)



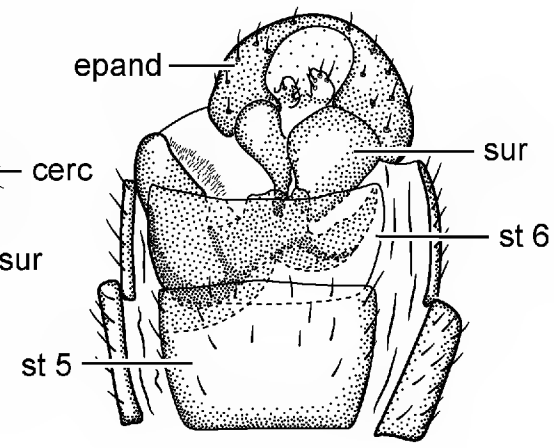
14 *Periscelis* ♂



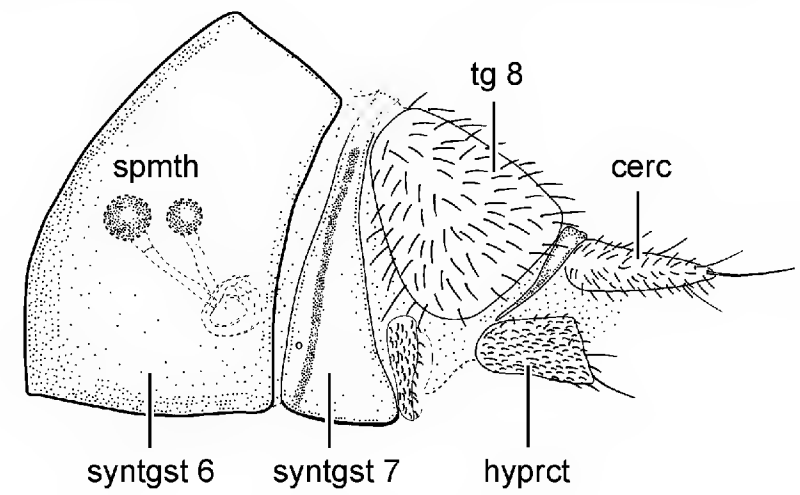
15 *Periscelis* ♂



16 *Cyamops* ♂



17 *Cyamops* ♂



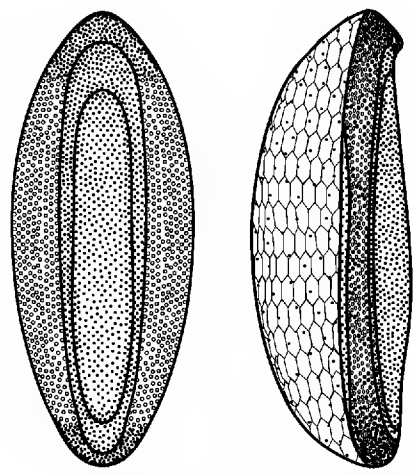
18 *Cyamops* ♀

Figs 91.12–18. Heads, male terminalia and female postabdomen of Periscelididae: (12) head of *Cyamops nebulosus* Melander, frontal view (non-Afrotropical); (13) same, *Stenomicra* (*Stenomicra*) *angustata* Coquillett (non-Afrotropical); (14) epandrium and internal male terminalia of *Periscelis stuckenbergi* Mathis & Freidberg, lateral view; (15) same, epandrium and cerci, posterior view; (16) epandrium and internal male terminalia of *C. nigeriensis* Baptista & Mathis, lateral view; (17) same, tergites and sternites 5–6, epandrium, surstylus and cerci, ventral view; (18) female postabdomen of *C. nigeriensis*, lateral view. Figs 12, 13 (Teskey 1987, figs 2, 3, as Aulacigastridae), Figs 14, 15 (Mathis & Friedberg 2012, figs 6, 7), Figs 16, 17 (after Baptista & Mathis 2000, figs 9, 8, respectively), Fig. 18 (Mathis & Papp 1998, fig. 20).

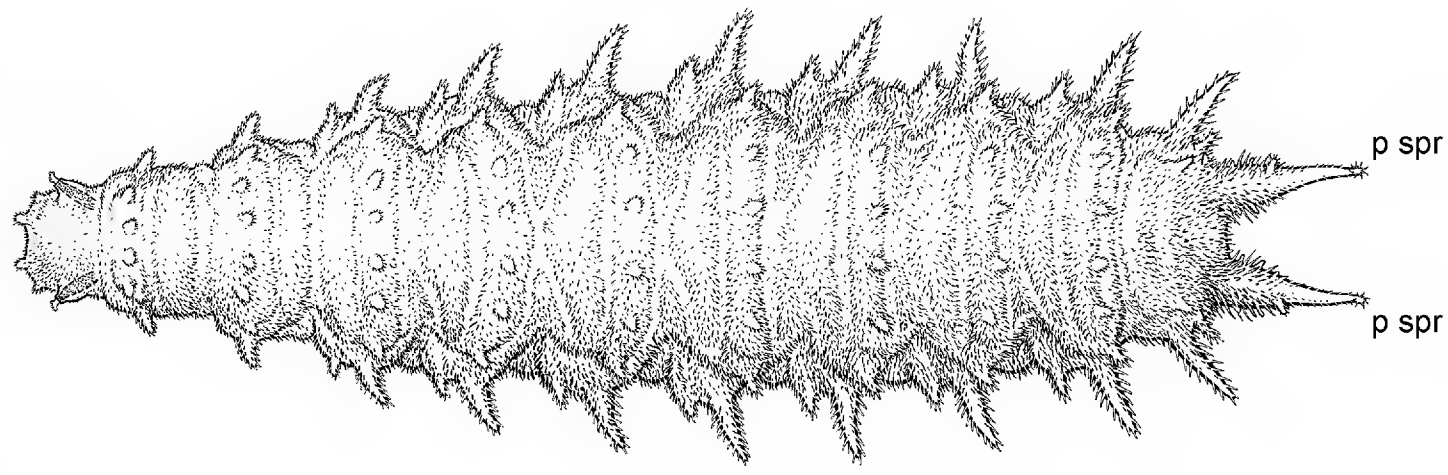
Abbreviations: cerc – cercus; ej apod – ejaculatory apodeme; epand – epandrium; frorb s – fronto-orbital setae; hypd – hypandrium; hypd com – hypandrial complex; hyprct – hypoproct; i vt s – inner vertical seta; o vt s – outer vertical seta; ph – phallus; phapod – phallapodeme; spmth – spermathecae; st – sternite; sur – surstylus; syntgst – syntergosternite; tg – tergite.

2010), *Cyamops*, *Planinasus* and *Stenomicra* grouped consistently with moderate support with the genus *Aulacigaster* Macquart and not with Periscelidinae. Moreover, the same analysis failed to find any support for a sister-group relationship between Periscelididae and Neurochaetidae. This study warrants further scrutiny and highlights the need to study the phylogeny of these groups in greater detail.

Papp (1984: 61) proposed Stenomicrinae for the genus *Stenomicra*. Grimaldi & Mathis (1993), Baptista & Mathis (1994) and Mathis & Papp (1998: 287) recognised two subfamilies (Periscelidinae and Stenomicrinae) in the Periscelididae, although the monophyly of only Periscelidinae is supported by the following putative synapomorphies: (1) occiput with silvery-white, micro-tomentose area immediately adjacent to posterior margin of compound eye (Fig. 3); (2) only 1 fronto-orbital seta, reclinate (Fig. 2); (3) mouth opening large (may be secondarily reduced in *Diopsosoma* Malloch, although difficult to determine, given severe lateral distensions of head); (4) costal vein (C) short, extended only to vein R_{4+5} (Fig. 8); (5) vein *CuA* reduced or absent; (6) postpronotal seta well-developed (Fig. 5); (7) spiracle 7 not free in female postabdomen; and (8) several characters of the male terminalia (Griffiths 1972: 116). The genera comprising Periscelidinae are those that Hennig (1969) included in his more restricted concept of the family, *viz*. *Diopsosoma*, *Marbenia* Malloch, *Neoscutops* Malloch, *Periscelis* and *Scutops* Coquillett. Baptista & Mathis (1994) presented evidence that the Neotropical genus *Planinasus* may be more closely related to Periscelidinae. Griffiths (1972: 121) considered the genera *Diopsosoma* and *Somatia* Schiner as Periscelididae. Mathis & Papp (1992) and Grimaldi & Mathis (1993), however, questioned this classification and Mathis (1993: 13) suggested that the male terminalia of *Somatia* are very similar to those of the Psilidae, demonstrating a close relationship with that family. In their review of *Diopsosoma*, Mathis & Rung (2004) provided a list of putative synapomorphies shared between this genus and other genera in Periscelidinae.



19 *Periscelis*



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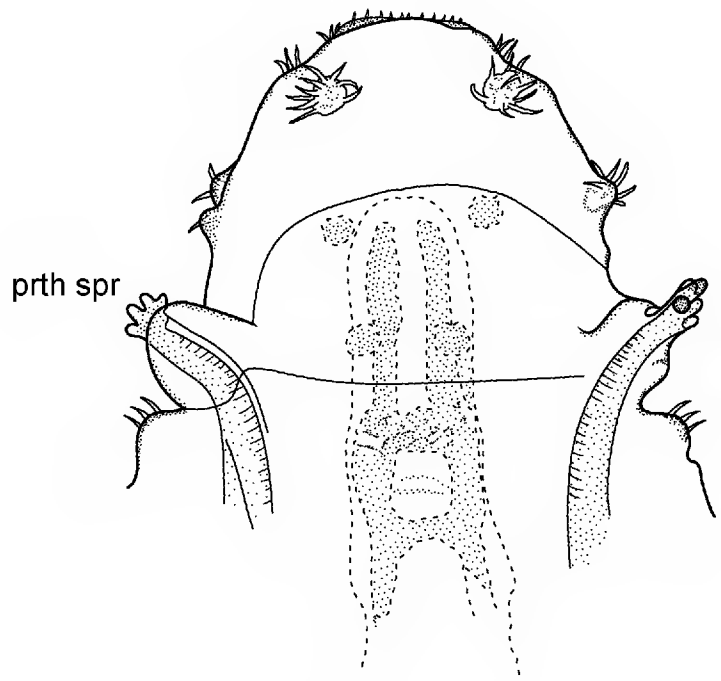
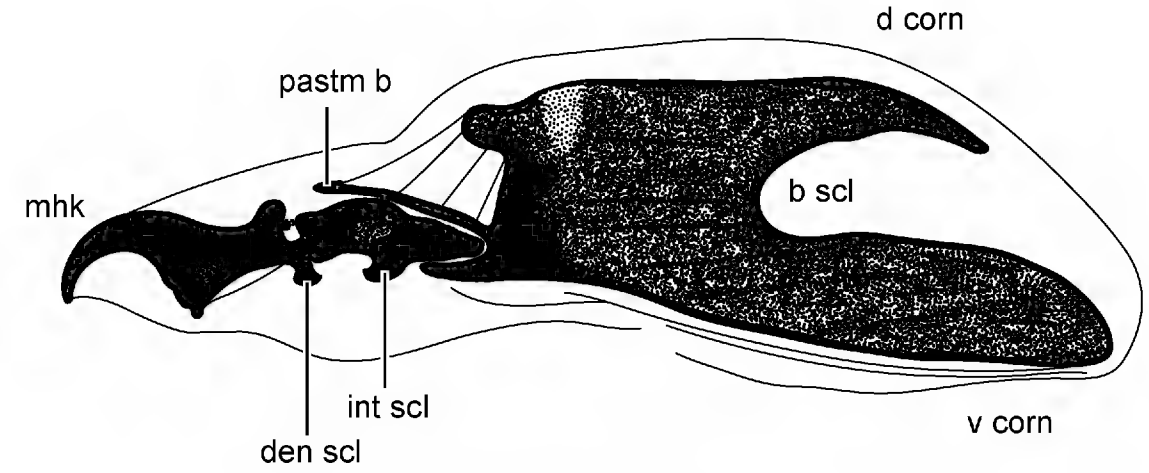


21 *Periscelis*



22 *Periscelis*

Figs 91.19–22. Immature stages of Periscelididae: (19) egg of *Periscelis nigra* (Zetterstedt), dorsal view (left), lateral view (right); (20) third-instar larva of *P. annulata* (Fallén), dorsal view; (21) same, cephalic and prothoracic segments with prothoracic spiracles, dorsal view; (22) cephaloskeleton of *P. annulata*, lateral view. Figs 19, 21, 22 (after Mathis & Papp 1998, figs 20, 21, 15, 16, respectively), Fig. 20 (McAlpine 1987, fig. 7).

Abbreviations: b scl – basal sclerite; d corn – dorsal cornu; den scl – dental sclerite; int scl – intermediate sclerite; mhk – mouthhook; p spr – posterior spiracle; pastm b – parastomal bar; prth spr – prothoracic spiracle; v corn – ventral cornu.

Although Stenomicrinae are recognised as a subfamily, evidence confirming its monophyly is vague or generally wanting. Thus, the genera here included in Stenomicrinae may eventually be placed elsewhere in the suprafamily Asteioinea (superfamily Opomyzoidea) and may not be as closely related to each other as the classification adopted here would infer. Stenomicrinae are characterised as follows: frons with 2 fronto-orbital setae, 1 reclinate, 1 usually proclinate; at least 1 vertical seta (apparently the lateral) present; postvertical setae usually lacking (present in some *Stenomicra*, where they are slightly divergent); ocellar setae lacking (Fig. 13) (present in fossil *Procyamops* Hoffeins & Rung); postpronotum frequently polished, lacking a well-developed seta; costal vein (C) extended to vein M_1; cell *cua* usually present, vein *CuA* usually well-developed (Figs 10, 11) (weakly developed or lacking in *Stenomicra*).

Identification

Periscelididae as defined here are a distinct family based on adult characters. Although 11 genera are currently recognised, only three have been recorded from the Afrotropical Region.

No single publication is available that deals with the entire Afrotropical Periscelididae fauna. The single species of *Periscelis* can be identified using Mathis & Freidberg (2012). The most recent key for *Cyamops* is provided by Rung & Ale-Rocha (2011). Species of *Stenomicra* can be separated using the key of Sabrosky (1975), the most recent contribution on the Afrotropical fauna of the genus. The patterns of infuscation on the wing and the colouration of legs can be used to identify species of *Cyamops* and *Stenomicra*, which can also be separated by colouration patterns on the body, although final species determinations must be based on examination of the male terminalia. Unfortunately, the male terminalia of Afrotropical *Stenomicra* have not been thoroughly investigated and descriptions and illustrations of the male terminalia are missing for most species.

Species of *Stenomicra* that have been traditionally grouped under *S. fascipennis* (Sabrosky, 1965) are currently being revised, some of which occur in Madagascar and other parts of the Afrotropics (Grimaldi 2009). Periscelidids are best micro-pinned in the field for later double-mounting (see Chapter 2).

Key to genera of Afrotropical Periscelididae

1. Head (e.g., Figs 12, 13) with 2 fronto-orbital setae; ocellar seta absent; wing (e.g., Figs 9–11) with costal vein (C) long, extended to vein M_1; vein *CuA* usually well-developed; usually with distinct cell *cua* (e.g., Fig. 9) (cell *cua* weakened, or lacking in some *Stenomicra*; e.g., Figs 10, 11); thorax with postpronotum without well-developed seta (STENOMICRINAE) 2

– Head (Figs 2–4) with 1 fronto-orbital seta; ocellar setae present, well-developed (Figs 2–4); wing (Fig. 8) with costal vein (C) short, extended only to vein R_{4+5}; vein *CuA* weak or lacking, cell *cua* weakened or absent; thorax with postpronotum with a well-developed seta (Fig. 5) (PERISCELIDINAE). . . . . *Periscelis* Loew

2. Head (Fig. 12) with 1 proclinate and 1 reclinate fronto-orbital setae; without inner vertical seta; thorax with metanotum not bulging; supra-alar seta present, well-developed; scutellar setae variable, but usually in 2 pairs; wing (Fig. 9) with distinct anal lobe and alula; vein *CuA* and cell *cua* present, well-developed . . . . . *Cyamops* Melander

– Head (Fig. 13) with fronto-orbital setae reclinate, or occasionally, inclinate, lacking proclinate seta; with inner vertical seta; thorax with metanotum bulging; without supra-alar seta; 1 pair of apical scutellar setae; wing (Figs 10, 11) with anal lobe greatly reduced; alula indistinct; vein *CuA* and cell *cua* often weak or absent . . . . . *Stenomicra* Coquillett 3

3. Wing vein R_{2+3} not reaching wing apex (Fig. 10); distance between apex of veins R_{2+3} and R_{4+5} at least 2 × as long as distance between apex of veins R_{4+5} and M_1; discal medial cell (*dm*) atrophied; crossveins *r–m* and *dm–m* approximated, distance between them < 2 × length of crossvein *dm–m* (Fig. 10); ventral fronto-orbital seta significantly shorter and weaker than dorsal seta . . . . . *Stenomicra sensu stricto*

– Wing vein R_{2+3} reaching wing apex (Fig. 11); distance between apex of veins R_{2+3} and R_{4+5} not longer than distance between apex of veins R_{4+5} and M_1; discal medial cell (*dm*) elongate; crossveins *r–m* and *dm–m* distant from each other, distance between them *ca* 2 × length of *dm–m* (Fig. 11); ventral fronto-orbital seta almost as long and strong as dorsal seta (Fig. 13). . . . . *Stenomicra* (*Podocera* Czerny)

Synopsis of the fauna

Periscelididae include 123 species in 11 genera globally. The Afrotropical fauna comprises 11 species in three genera.

***Cyamops* Melander** (Stenomicrinae). A virtually cosmopolitan genus of 34 described species with its greatest diversity in the Australasian Region. The Afrotropical fauna includes three species that have been recorded from Madagascar, Namibia and Nigeria. Baptista & Mathis (2000) and Rung & Ale-Rocha (2011) described all Afrotropical species. The immature stages remain unknown. Rung & Ale-Rocha (2011) published the most recent identification key to Afrotropical species.

***Periscelis* Loew** (Periscelidinae). A virtually cosmopolitan genus of 18 described species, mostly from the New World

and Palaearctic Region. A single species, *Periscelis stuckenbergi* Mathis & Freidberg, 2012, was described from Ethiopia (Mathis & Freidberg 2012). The immature stages of *P. stuckenbergi* remain unknown.

***Stenomicra* Coquillett** (Stenomicrinae)**.** A virtually cosmopolitan genus of 39 described species, being most diverse in the Neotropics, where over 100 species await description (D. Grimaldi, pers. comm. 2013). Although eight species are known from the Afrotropics (Mathis & Rung 2011), it is possible that many more will be found in the future. Two subgenera have been recognised: *Stenomicra sensu stricto* and *S.* (*Podocera*) (Sabrosky 1975). Most described species of *Stenomicra* in the Afrotropics belong in *S.* (*Podocera*) (six of eight species). Immature stages of Afrotropical species remain unknown. Sabrosky (1975) published the most recent identification key to Afrotropical species.

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ASTEIIDAE 92

(Asteiid Flies)

Amnon Freidberg† and Ariel-Leib-Leonid Friedman

Fig. 92.1. Female of *Asteia* sp. (Madagascar) (photograph © S.A. Marshall).

Diagnosis

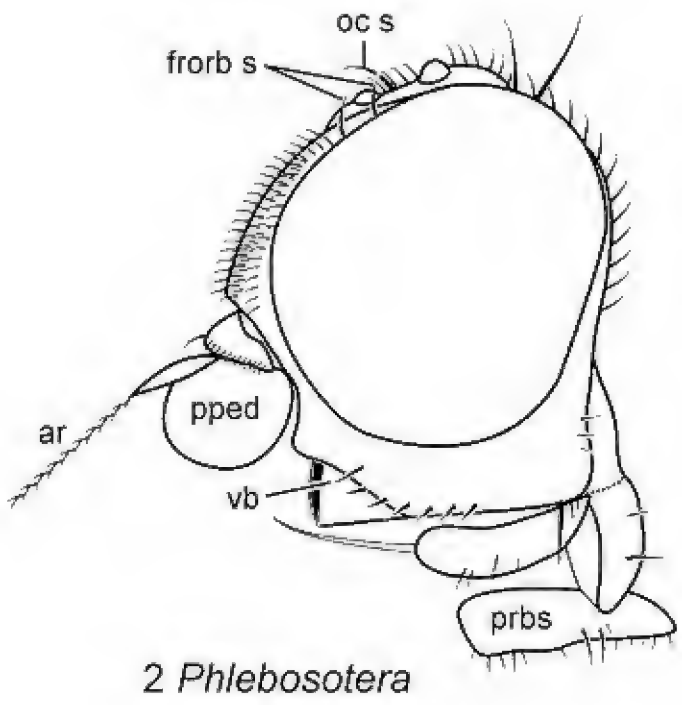
Small-sized (body length: 1–5 mm), generally weakly sclerotised acalyptrate flies (Fig. 1); colouration varies from predominantly yellow to predominantly black, but more or less elaborate and contrasting pattern usually present on some or all major body parts, including the abdominal pleural membrane.

Head oval (Fig. 2) or rectangular (Fig. 3) in lateral view, with 0–2 short to long fronto-orbital setae; ocellar setae well-developed or reduced to about same size as fronto-orbital setulae (Figs 2, 3); male frons with variously formed interfrontal stripes (Fig. 4); 1 distinct vibrissa present (Figs 2, 3); antenna short, with postpedicel more or less rounded or squarish (Figs 2–4); arista usually well-developed, with short (Figs 2–4), to long alternating branches (microtrichia, Fig. 5), sometimes reduced (Fig. 6) or lacking; proboscis short, with fleshy labella (Figs 2, 3).

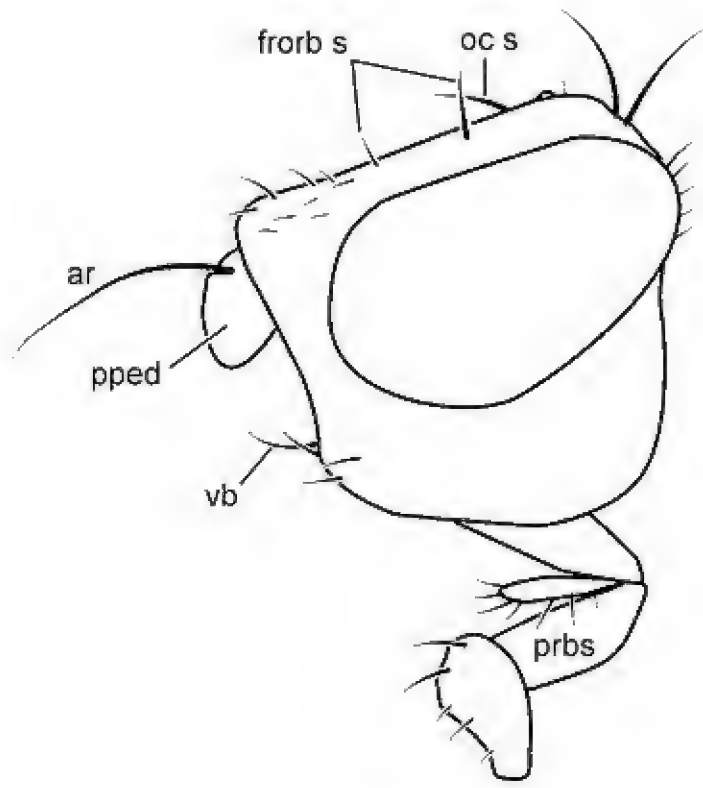
Thorax with 1–4 dorsocentral setae, if 4, then anterior dorsocentral seta presutural (Afrotropical species with at most 2 postsutural dorsocentral setae); posterior dorsocentral seta sometimes accompanied by anterior row of *ca* 6 long setulae or by numerous short setulae. Scutellum *ca* 0.25–0.33 × as long as scutum, convex, usually with 2 pairs of setae; basal seta slightly or distinctly shorter than apical seta or lacking; acrostichal setulae either absent or forming 2 rows; pleura, except katepisternum, without setae; anepisternum setulose only in *Phlebosotera* Duda. Wing (Figs 7, 8) usually elongate, covering abdomen and extended beyond it when at rest; vein R_{2+3} short, ending at apex of vein R_1 or slightly distal to it, except in non-Afrotropical *Leiomyza* Macquart, in which it reaches distal 0.75 of wing; vein M_1 curves posteriorly, then anteriorly ("concave"), distally convergent with vein R_{4+5}; crossvein *dm–m* present (Fig. 7) or lacking (Fig. 8); cell *cua* and vein *CuA+CuP* at least indicated as fold (Fig. 7) or lacking (Fig. 8); alula either well-developed, with marginal cilia (Fig. 7) or rudimentary and bare (Fig. 8). Legs usually without overt features, except hind coxa in male of *P. nigriseta* Sabrosky, 1956, with broad and flat posterior extension.

Abdominal tergites weakly sclerotised; spiracle 2–6 situated in tergites; spiracle 7 lacking; male terminalia asymmetrical in most taxa (Fig. 9), symmetrical in non-Afrotropical *Leiomyza*; surstylus fused with epandrium; phallus (Fig. 10) usually large compared to body size, heavily sclerotised and structurally complex, rarely

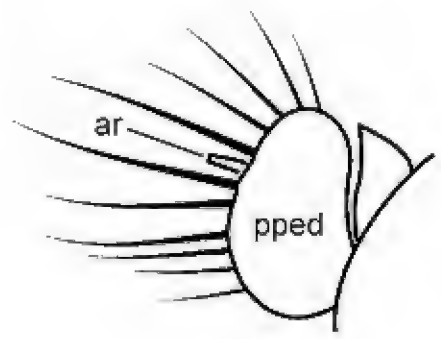
Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2021. Manual of Afrotropical Diptera. Volume 3. Brachycera—Cyclorrhapha, excluding Calyptratae. *Suricata* 8. South African National Biodiversity Institute, Pretoria; pp. 1989–1994.



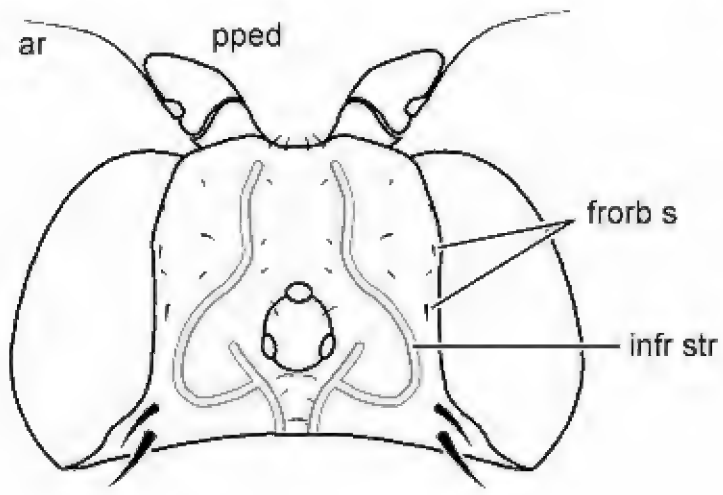
2 *Phlebosotera*



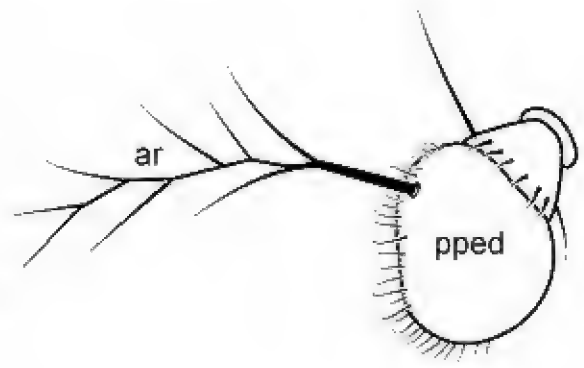
3 *Asteia* (*Eisentrautius*)



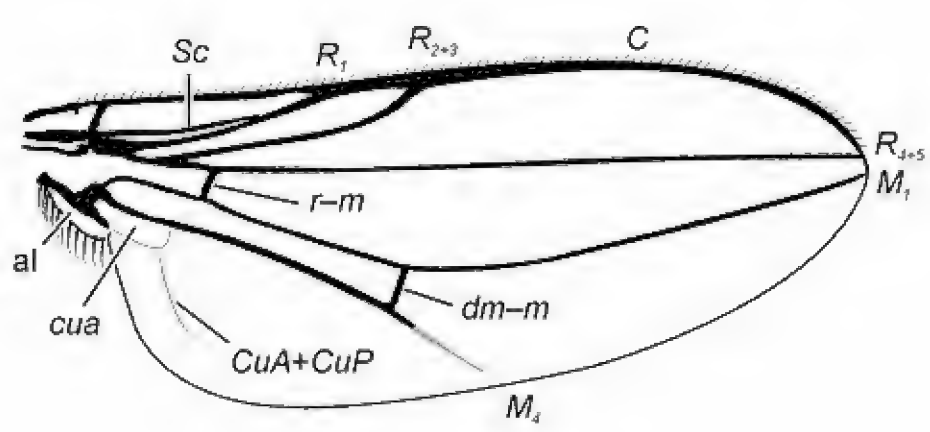
6 *Anarista*



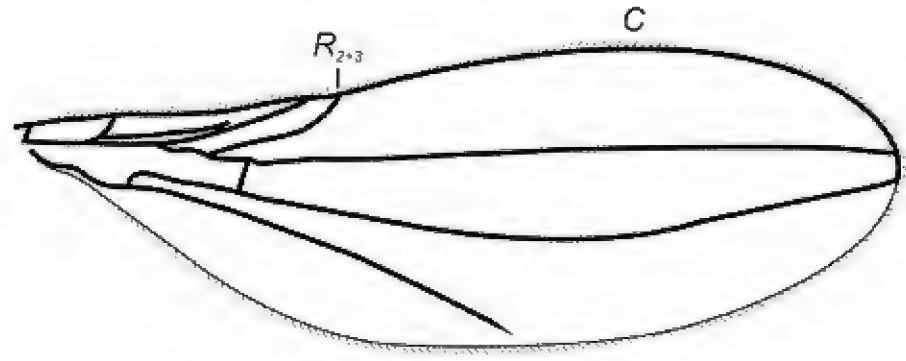
4 *Phlebosotera*



5 *Asteia*



7 *Phlebosotera*



8 *Asteia*

Figs 92.2–8. Heads, antennae and wings of Asteiidae: (2) head of *Phlebosotera clypeata* Freidberg & Carles-Tolrá, lateral view (non-Afrotropical); (3) same, *Asteia* (*Eisentrautius*) sp. (non-Afrotropical); (4) same, *P. nigriseta* Sabrosky, dorsal view; (5) antenna of *Asteia* sp., lateral view; (6) same, *Anarista* sp.; (7) wing of *Phlebosotera* sp., dorsal view; (8) same, *Asteia* sp. Figs 2, 7 (after Freidberg & Carles-Tolrá 2011, figs 3, 5).

Abbreviations: al – alula; ar – arista; *C* – costal vein; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *dm–m* – discal medial crossvein; frorb s – fronto-orbital seta; infr str – interfrontal stripe; M_1 – first branch of media; M_4 – fourth branch of media; oc s – ocellar seta; pped – postpedicel; prbs – proboscis; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Sc* – subcostal vein; vb – vibrissa.

small, membranous, ribbon-like and structurally simple; female terminalia simple, although segment 7 sometimes developed as incomplete oviscape; 2 sclerotised spermathecae present.

Adult Asteiidae are superficially similar to some Anthomyzidae (see Chapter 87), Periscelididae (*Stenomicra* Coquillett) (see Chapter 91) and Drosophilidae (see Chapter 106), but these families do not have the combination of a concave wing vein M_1 (Figs 7, 8), alternating branches on the arista (Fig. 5) and the male head with interfrontal stripes (Fig. 4).

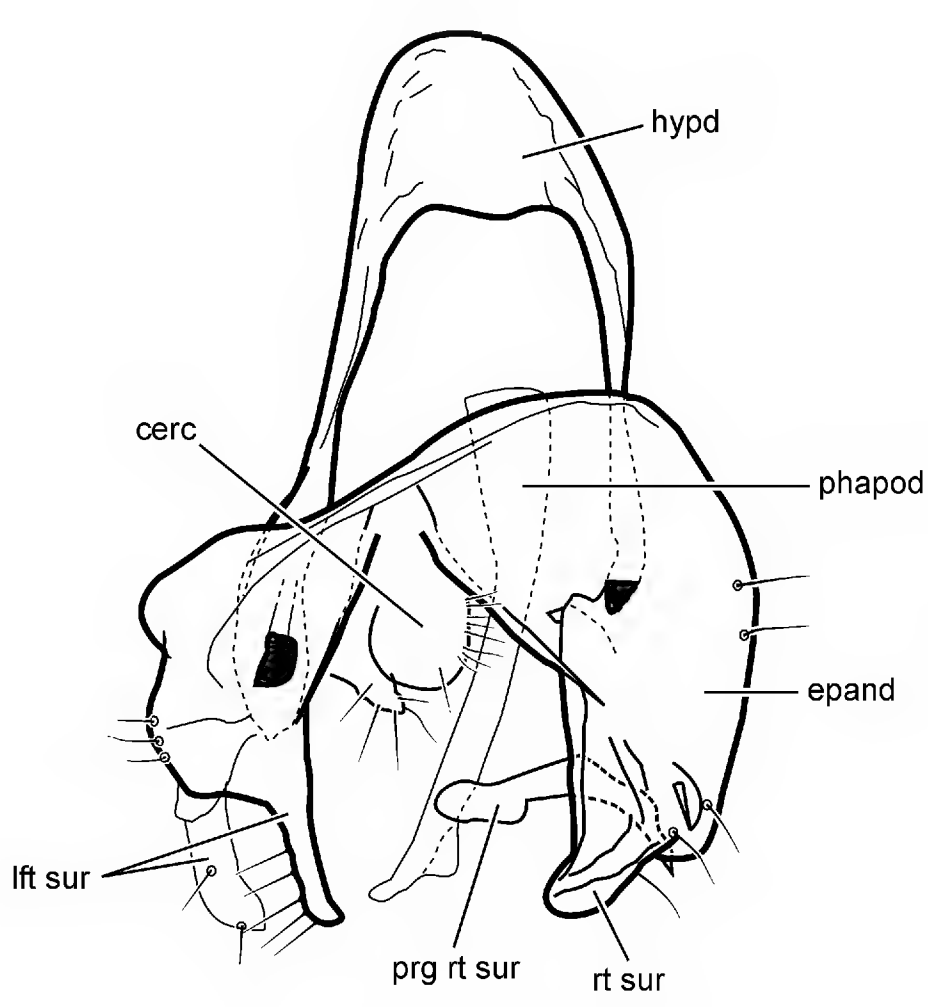
Biology and immature stages

Little is known regarding the biology of asteiids and almost nothing about the biology of Afrotropical species. Phytophagous (*Asteia* Meigen), fungivorous (*Leiomyza*) and saprophagous (*Phlebosotera*) species are known (Freidberg 2002; Papp 1998: 299) and immatures belonging to these three taxa are either described (Papp 1998: 297) or are in the process of being described (Freidberg, in prep.). Adult asteiids are generally uncommon in collections, despite the fact that they may be abundant under certain natural conditions, such as on particular trees (e.g., pine (*Pinus*, Pinaceae), tamarisk (*Tamarix*, Tamaricaceae), oak (*Quercus*, Fagaceae) and banana (*Musa*, Musaceae)), on herbaceous vegetation and in entrances to caves. Courtship and mating are sometimes elaborate, including mating trophallaxis (Freidberg 1984; Freidberg & Carles-Tolrá 2011).

Immatures of only two species have been thoroughly described to date; both, *Asteia* sp. and *Leiomyza dudai* Sabrosky, 1956, are non-Afrotropical (Papp 1992, 1998: 297). In this account knowledge of these two species is briefly summarised, together with original data (including illustrations) of two additional non-Afrotropical species (*Asteia* (*Eisentrautius* Enderlein) sp. and *Phlebosotera* sp.). *Eisentrautius* should be reinstated from synonymy to include this and several other species.

The egg of *L. dudai* was described by Papp (1998: 297), who also cited measurements for eggs of other species. He noted that eggs of Asteiidae are relatively large, *i.e.*, about as long as the female abdomen, a feature that can easily be observed in many fresh or preserved specimens. The eggs are white, *ca* 0.4–0.5 mm in length and *ca* 3.5–4.0 × as long as wide.

Only the third-instar larva (Figs 11–13) has received detailed treatment. In the studied species the fully grown larva is *ca* 2–3 mm in length and is translucent whitish, without overt features, such as tubercles, although the cuticular surface may be wrinkled with small bumps. The cephaloskeleton (Fig. 11) has the mouthhooks narrow to robust, more or less sickle-shaped in *Phlebosotera*, with three small preapical teeth ventrally. The intermediate sclerite is more or less elongated, *ca* 3.5–6.0 × as long as high. The labial sclerite is absent (Papp 1998: 297) and the parastomal bar is either lacking, or not well-differentiated from the intermediate sclerite. The dental sclerite is small and inconspicuous. The prothoracic spiracle (Fig. 12) has three



9 *Phlebosotera* ♂

10 *Phlebosotera* ♂

Figs 92.9–10. Male terminalia of Asteiidae: (9) epandrium and associated structures of *Phlebosotera clypeata* Freidberg & Carles-Tolra, posterior view; (10) same, phallus, unknown view. Figs 9, 10 (after Freidberg & Carles-Tolra 2011, figs 6, 7).

Abbreviations: cerc – cercus; epand – epandrium; hypd – hypandrium; lft sur – left surstylus; phapod – phallapodeme; prg rt sur – prong of right surstylus; rt sur – right surstylus.

spiracular openings in *Phlebosotera*, four in *Asteia* sp. and up to 7–8 openings in *L. dudai*. The atrium of the prothoracic spiracle is *ca* 4–5 × as long as wide in at least two of the three studied genera. The posterior spiracles are either closely approximated or far apart (Fig. 13), with three round spiracular openings, forming a right angle and four groups of large densely branched peristigmatic tufts.

The puparium is yellow to brown in colour, *ca* 2 mm in length (Fig. 14), is strongly wrinkled, with the openings of both the prothoracic and posterior spiracles borne on short fleshy tubercles, otherwise without overt features.

Economic significance

Asteiidae have no known economic significance.

Classification

The relationships of this family have historically been obscure. Hennig (1973: 59) treated Asteiidae as part of his superfamily Anthomyzoidea and within it as part of the Periscelididea family-group (with Aulacigastridae, Periscelididae and non-Afrotropical Teratomyzidae). Griffiths (1972: 190) tentatively proposed a closer relationship of Asteiidae, Opomyzidae and Trixoscelididae (the last-named family considered a subfamily of Heleomyzidae in this *Manual*), based on the loss of abdominal spiracle 7 in both sexes. McAlpine (1989: 1454) considered asteiids to be part of his superfamily Opomyzoidea, including some of the families in Hennig's and Griffiths' groups, in particular corresponding to Hennig (1973: 59) and Griffiths (1972: 190) and agreeing with Hennig in recognising the phylogenetic relationship among Asteiidae, Periscelididae, Aulacigastridae and Teratomyzidae in his suprafamily Asteioinea. Based on the molecular analysis of Winkler *et al.* (2010) and Wiegmann *et al.* (2011), the sister-group of Asteiidae is Fergusoninidae (or Australasian gall flies), both not assigned to any superfamily. Since the classification of the acalyptrate Diptera is still developing, additional changes to these groups are anticipated.

Within the family, Sabrosky (1956) proposed the subfamilies Asteiinae (as Asteinae) and Sigaloessinae and in the same publication gave the most comprehensive identification key to the world genera. *Anarista* Papp was subsequently added to the family (Papp 1972). Freidberg (2002) transferred *Leiomyza* from Sigaloessinae to the new subfamily Leiomyzinae, and made it the sole representative of this subfamily, and included all other genera in Asteiinae. The latter subfamily was divided into two tribes, mostly corresponding to Sabrosky's subfamilies, although with the exception noted above (Friedberg, in prep.; and see identification key below). Based on cladistic analysis, *Anarista*, which shares characters of both tribes, should be assigned to Sigaloessini (Freidberg 2002). Papp (2013) provided an identification key to Old World genera.

Identification

The most recent identification resource for Old World species is the synopsis by Sabrosky (1956). This work is outdated, however, and much additional work is required on the family.

Several new species, primarily in *Asteia*, have been described in the past few decades (Carles-Tolrá 1998; Deeming 2010: 641; Forrest & Wheeler 2002; Freidberg & Carles-Tolrá 2011; Grimaldi 2009; Sueyoshi 2003; Yang & Zhang 1996: 491), including *Asteia arabica* Deeming, 2010 and *A. vanharteni* Deeming, 2010, from the Afrotropical parts of the Arabian Peninsula. Hence, Sabrosky's (1956) identification key to Afrotropical species of *Asteia* remains the only identification key and is still fairly helpful for identification of the eight Afrotropical species then known, although it is missing two species that had been previously described (*A. decepta* Becker, 1908 and *A. nigerrima* Séguy, 1938).

The genus *Leiomyza* Macquart is not recorded from the Afrotropical Region, but is included in the identification key below, as it is likely to be discovered there in the future. Asteiidae are best micro-pinned in the field for later double-mounting (see Chapter 2).

Key to genera of Afrotropical Asteiidae

1. Wing vein R_{2+3} reaching costal vein (C) at *ca* distal 0.75 of wing length; male terminalia with epandrium symmetrical (Holarctic Realm and Australasian Region) (LEIOMYZINAE) . . . . . [*Leiomyza* Macquart]
– Wing vein R_{2+3} reaching costal vein (C) at < ½ wing length (e.g., Figs 7, 8); male terminalia with epandrium asymmetrical (e.g., Fig. 9) (worldwide) (ASTEIINAE) 2
2. Wing without crossvein *dm–m*; alula absent, margin without cilia (Fig. 8) (ASTEIINI) . . . *Asteia* Meigen
– Wing with crossvein *dm–m*; alula present, margin with cilia (e.g., Fig. 7) (SIGALOESSINI). 3
3. Thorax with anepisternum setulose; antennal arista normal, distinct (Fig. 2) . . . . . *Phlebosotera* Duda
– Thorax with anepisternum bare; antennal arista vestigial, barely visible (Fig. 6). . . . . *Anarista* Papp

Synopsis of the fauna

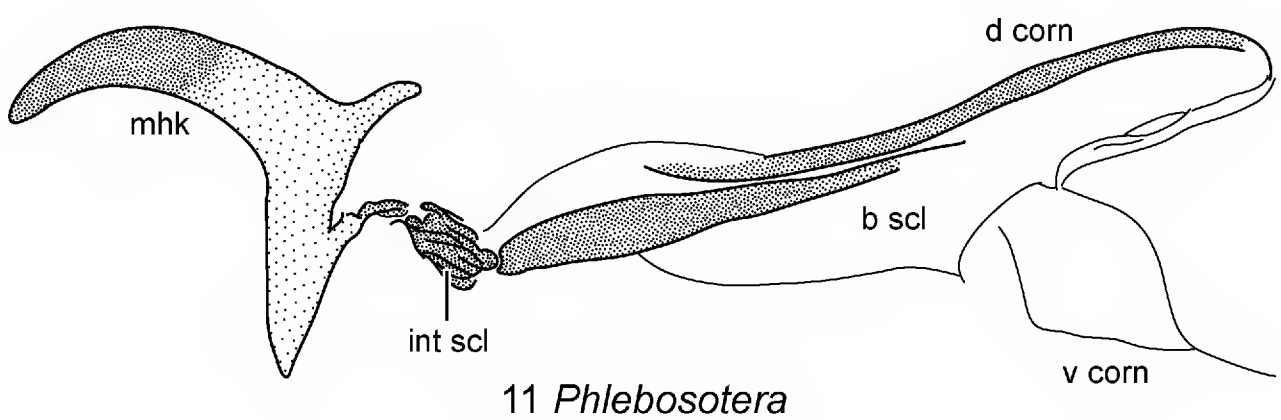
Twenty species in three genera of this small family are recorded from the Afrotropical Region.

***Asteia* Meigen** (Asteiinae: Asteiini)**.** A genus of 80 described species, occurring in all zoogeographical regions, except Antarctica. Twelve species are known from the Afrotropics and 2–3 apparently undescribed species are present in collections (A. Freidberg,

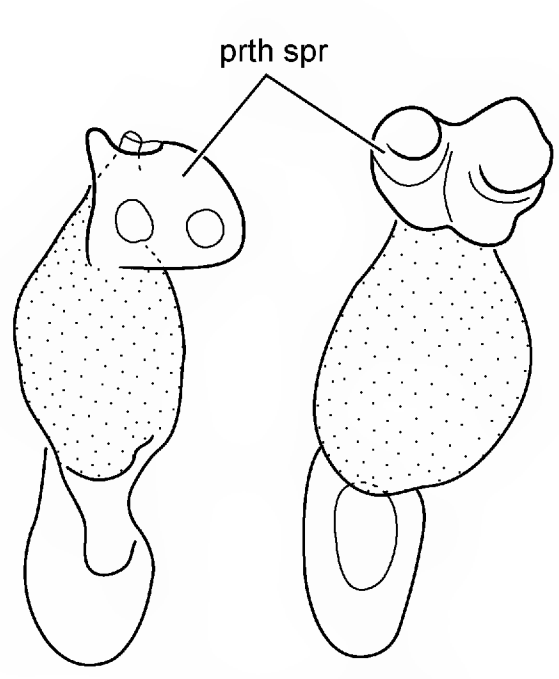
pers. obs.). Of the twelve recorded species, ten are endemic to the region. Half of the species are recorded only or predominantly from Southern Africa. Five species are recorded from the Arabian Peninsula (Oman, United Arab Emirates and Yemen). *Asteia nigroscutellata* Duda, 1927 is widely distributed throughout East and Southern Africa, Comoros and Madagascar. *Asteia amoena* Meigen, 1830, a widespread Palaearctic species, was recorded once from Mt Elgon (Séguy 1938), but the existence of numerous specimens in collections (*e.g.*, Tel Aviv University, Israel), indicates that it occurs widely in East Africa. *Asteia decepta* Becker, 1908 was described from the Canary Is., and also recorded from Cabo Verde and Yemen (Deeming 2010; Sabrosky 1956), but the conspecificity of the specimens from both archipelagos needs confirmation. Nothing is known regarding the biology and immature stages of Afrotropical species. The most recent identification key to Afrotropical species was published by Sabrosky (1956) and to Arabian species specifically by Deeming (2010).

Anarista **Papp** (Asteiinae: Sigaloessini)**.** A predominantly Afrotropical genus of five known species. Four species are known from the Afrotropics, three of which are currently known only from their type localities in Central and West Africa. One species, *A. vittata* Sabrosky, 1977, was recorded from Nigeria (Sabrosky 1977) and also from Oman and United Arab Emirates in the Arabian Peninsula (Deeming 2010). An unidentified species was recorded from Papua New Guinea in the Australasian Region by Sabrosky (1989), further expanding the known distribution of the genus. Seven undescribed species, all strictly Afrotropical, have been studied in collections (primarily in the Steinhardt Museum of Natural History, Tel Aviv University, Israel). *Anarista* includes small- to tiny-sized species (*e.g.*, 1 mm in length), that are sometimes difficult to see in a sweep net. They appear to favour large monocotyledons, such as banana leaves, to rest on. Discovery of numerous additional species from tropical Africa is expected. Sabrosky (1977) published the only identification key to Afrotropical species.

Phlebosotera **Duda** (Asteiinae: Sigaloessini)**.** The second largest genus in the family, with 20 described species; it occurs in all zoogeographical regions, except Antarctica. Species are elusive, however, and many are known from single specimens. Four species have been recorded from the Afrotropics, two from Nigeria, one from Malawi and one from Namibia. Two additional species occur in Namibia, of which at least one is undescribed. Nothing is known regarding the biology and immature stages. An identification key to Afrotropical species was published by Sabrosky (1956) and to Arabian species specifically by Deeming (2010).



11 *Phlebosotera*



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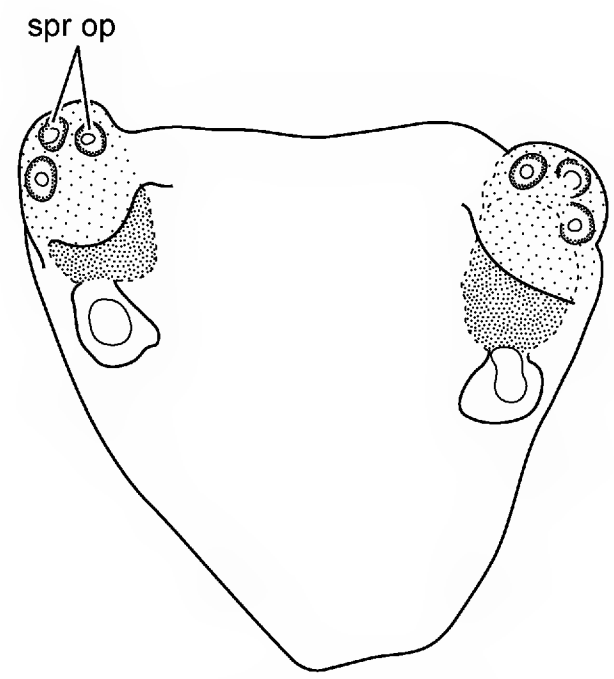
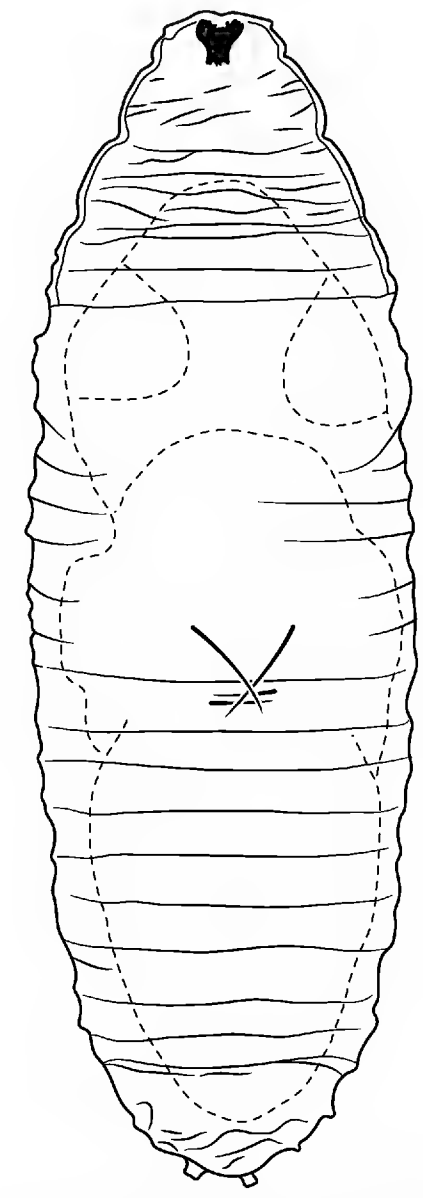


13 *Phlebosotera*



14 *Asteia* (?*Eisentratius*)

Figs 92.11–14. Immature stages of Asteiidae: (11) cephaloskeleton of *Phlebosotera* sp., lateral view; (12) same, prothoracic spiracles, lateral view; (13) same, posterior spiracles, caudal view; (14) habitus of puparium of *Asteia* (?*Eisentratius*) sp., dorsal view.

Abbreviations: b scl – basal sclerite; d corn – dorsal cornu; int scl – intermediate sclerite; mhk – mouthhook; prth spr – prothoracic spiracle; spr op – spiracular opening; v corn – ventral cornu.

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CARNIDAE 93

(Carnid Flies, Bird Flies or Filth Flies)

John E. Swann and Jens-Hermann Stuke

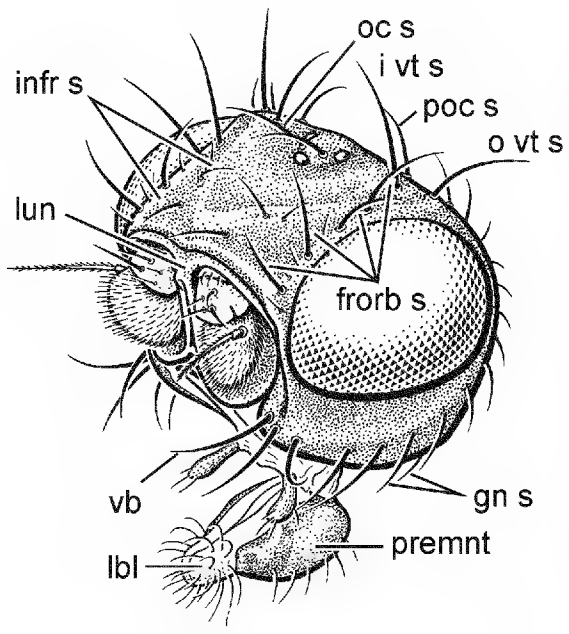
Fig. 93.1. Male and female *Carnus hemapterus* Nitzsch (non-Afrotropical) (photograph © S.A. Marshall).

Diagnosis

Minute-sized (body length: 1.0–2.5 mm), mainly black to brownish acalyptrate flies (Fig. 1), with distinct setulae on abdominal membrane, distinct head setation (2 lower inclinate, 2 upper lateroclinate fronto-orbital setae, 1 or 2 interfrontal setae), presence of both humeral and subcostal wing breaks and deeply recessed antennae, with microtrichose arista; often associated with birds' nests, carrion, small mammal runs and droppings, decaying organic matter, fungi and dung.

Head (Figs 2–4) black, with frons, face and gena often more or less yellow; compound eye without pubescence; Afrotropical genera with 2 lower inclinate fronto-orbital setae, 2 upper lateroclinate fronto-orbital setae, 2 vertical setae, 1–2 interfrontal setae (including parallel to cruciate supralunular setae), 1 pair of ocellar setae; postocellar setae variable, but usually small, parallel or divergent (Fig. 2); gena generally broad, with 1 strong vibrissa, 2 subvibrissal setae and 1–5 strong genal setae; lunule without setae; antennae usually deeply recessed in antennal fovea, separated by narrow, more or less prominent, facial carina; antennal postpedicel rounded; arista short, at most microtrichose; palpus generally moderately small; proboscis usually short, prementum thick, bulbous (Fig. 2), sometimes elongated in *Hemeromyia* Coquillett.

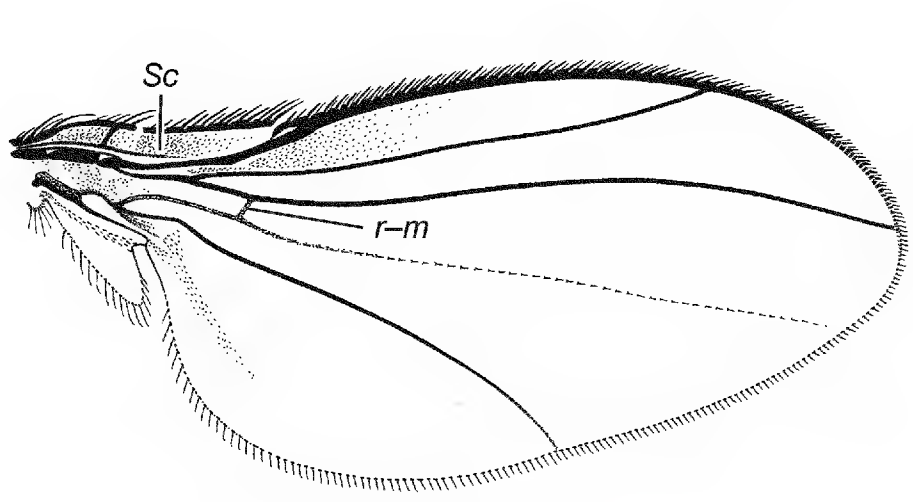
Thorax with 1 proepisternal seta, 1 proepimeral seta, 1 large and 1 small postpronotal seta, 1 presutural supra-alar seta and



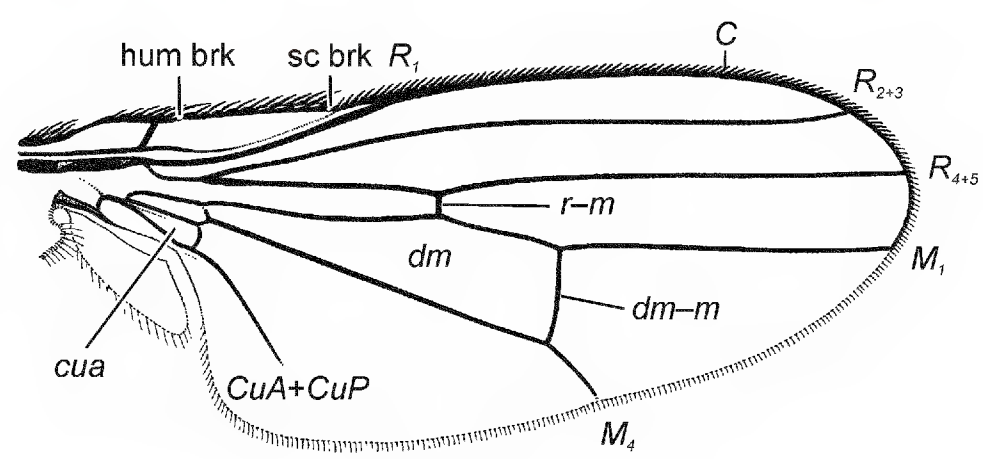
2 *Carnus*

3 *Hemeromyia*

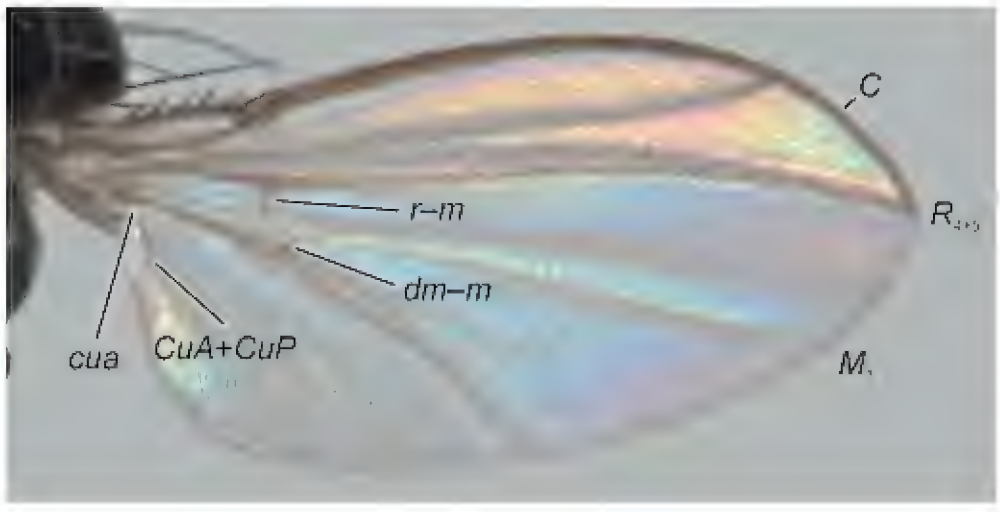
4 *Meoneura*



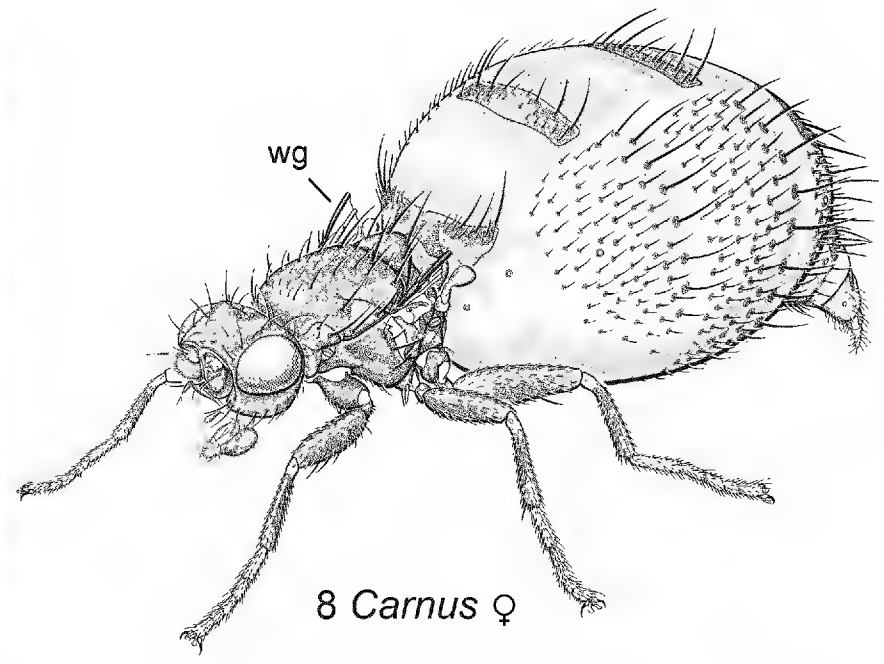
5 *Carnus*



6 *Hemeromyia*



7 *Meoneura*



8 *Carnus* ♀

Figs 93.2–8. Heads, wings and habitus of Carnidae: (2) head of *Carnus hemapterus* Nitzsch, anterolateral view (non-Afrotropical); (3) same, *Hemeromyia obscura* Coquillett (non-Afrotropical); (4) same, *Meoneura* sp.; (5) wing of *C. hemapterus*, dorsal view; (6) same, *Hemeromyia* sp. (non-Afrotropical); (7) same, *Meoneura* sp.; (8) habitus of *C. hemapterus*, anterolateral view ♀. Figs 2, 5, 6, 8 (Sabrosky 1987, figs 4, 3, 2, 1, respectively), Figs 3, 4, 7 (© Trustees of Natural History Museum, London).

Abbreviations: *C* – costal vein; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *dm* – discal medial cell; *dm–m* – discal medial crossvein; frorb s – fronto-orbital setae; gn s – genal setae; hum brk – humeral break; i vt s – inner vertical seta; infr s – interfrontal setae; lbl – labellum; lun – lunule; M_1 – first branch of media; M_4 – fourth branch of media; o vt s – outer vertical seta; oc s – ocellar seta; poc s – postocellar seta; premnt – prementum; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Sc* – subcostal vein; sc brk – subcostal break; vb – subvibrissa; wg – wing (base).

1 postsutural supra-alar seta, 2 notopleural setae, 1–4 dorsocentral setae, 1 prescutellar acrostichal seta, 1 apical and 1 lateral scutellar seta; 1 upcurved ventral anepisternal seta; 2 katepisternal setae. Scutellum with disc bare. Wing membrane (Figs 5–7) hyaline (wing normally broken-off short distance from costagial break in *Carnus* Nitzsch (Fig. 8)); costal vein (*C*) with humeral and subcostal breaks (Fig. 6); subcostal vein (*Sc*) complete, but generally short and weak distally (Fig. 5), joining costal vein (*C*) separately from vein R_1; vein R_1 without setae; veins R_{4+5} and M_1 parallel; venation more or less reduced in *Carnus* and *Meoneura* Rondani; halter usually white. Legs with tibiae lacking dorsal preapical setae.

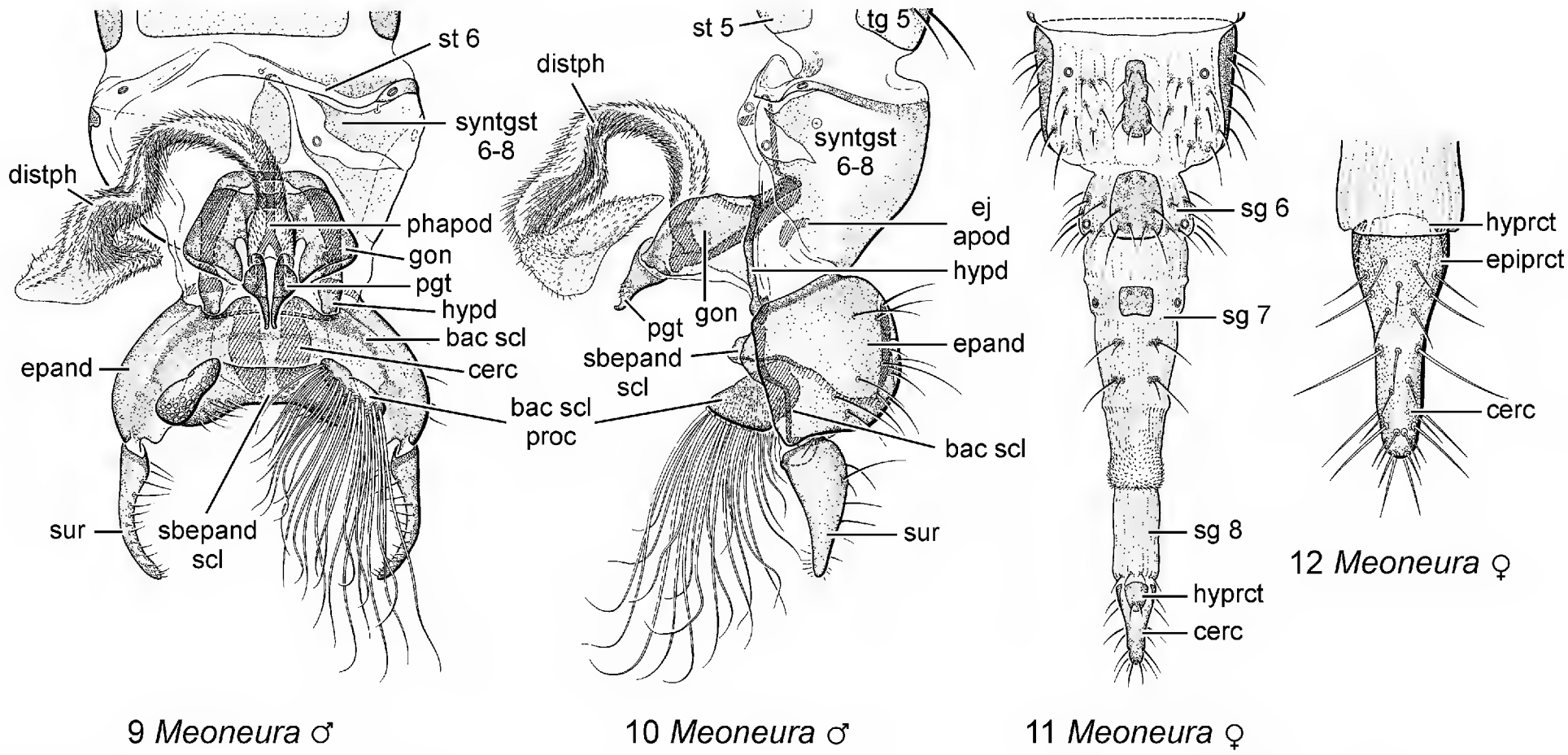
Abdomen with reduced sclerites in *Carnus* only (Figs 1, 8); distinct setulae on pleural membrane; sternite 7 and 8 fused to different degrees; male terminalia (Figs 9, 10) with various modifications of surstyli, bacilliform sclerite and subepandrial sclerite and therefore usually species-specific; subepandrial sclerite enlarged and partially fused with epandrium; surstyli not fused to epandrium; some *Meoneura* with bacilliform sclerite process and some with lamella (*sensu* Papp 1998: 213) of unknown origin close to surstylus; epandrium and hypandrium with flexible connection; postgonites present; distiphallus usually long, membranous, with different patterns of setulae, spinules or sclerotisations; female postabdomen telescopic, with cerci fused into pointed projection (Figs 11, 12); 2 spermathecae present.

Egg spindle-shaped, light brown to white in colour, without sculpture, with longitudinal keels. Larva (Fig. 13) whitish and puparium (Figs 17, 18) brown to golden; with creeping welts distinctly developed in some *Carnus*, but without spicules; surface at least partly with dense setulae in *Carnus* (Figs 13, 17); cephaloskeleton (Fig. 14) with developed, pointed mouthhooks, without dorsal connection; basal sclerite sclerotised with dorsal bridge and dorsal and ventral cornua; parastomal bar developed; intermediate sclerite distinct, H-shaped; prothoracic spiracles with 3 spiracular papillae in *Meoneura* (Fig. 15), > 3 in *Carnus*; posterior spiracles widely separated, each with 3 digitiform protuberances in *Carnus* and *Meoneura* (*e.g.*, Fig. 16), or without such protuberances in *Hemeromyia*; peristigmatic tufts absent; longitudinal anal opening flanked by small protuberance (which may represent reduced anal papillae).

Some Milichiidae (see Chapter 95) may be confused with Carnidae, but milichiids have setae on the lunule, most have the palpus and proboscis markedly elongated, the female cerci are unfused and the males lack postgonites, while carnids lack setae on the lunule, the palpi are only moderately long, the proboscis is usually not elongate, the female has fused cerci and the male possesses postgonites.

Biology and immature stages

The biology of most carnid species remains unknown, although the majority of species are saprophagous as larvae, feeding in dung, carrion, fungi, mammal and birds' nests and in



Figs 93.9–12. Male terminalia and female abdomen of Carnidae: (9) male terminalia of *Meoneura obscurella* (Fallén), ventral view (non-Afrotropical); (10) same, left lateral view; (11) same, female abdomen, ventral view; (12) same, dorsal view. Figs 9–12 (Sabrosky 1987, figs 7, 8, 5, 6, respectively).

Abbreviations: cerc – cercus; bac scl – bacilliform sclerite; bac scl proc – bacilliform sclerite process; distph – distiphallus; ej apod – ejaculatory apodeme; epand – epandrium; epiprct – epiproct; gon – gonopod; hypd – hypandrium; hyprct – hypoproct; pgt – postgonite; phapod – phallapodeme; sbepand scl – subepandrial sclerite; sg – segment; st – sternite; sur – surstylus; syntgst – syntergosternite; tg – tergite.

decaying vegetation and these are the substrates that adults are commonly found in association with or larvae are reared from (e.g., Büttiker 1975; Chandler 2019; Hackman & Meinander 1979; Hennig 1950; Sabrosky 1959; Valera *et al*. 2006*a*). The genera *Carnus* and *Hemeromyia* are most commonly encountered when specifically investigating abandoned birds' nests (e.g., Grimaldi 1997; Valera *et al*. 2006*a*). Only a few larval records are known from the Afrotropical Region: *Meoneura nigrohalterata* Papp, 2013, was collected from dung of the African bush elephant, *Loxodonta africana* (Blumenbach) (Elephantidae) (Papp 2013); *M. prima* (Becker, 1903) and *M. australis* Deeming, 1997, were found in association with runs of the Namaqua rock mouse, *Aethomys namaquensis* (A. Smith) (Muridae), probably breeding in their droppings (Kirk-Spriggs 2001) and in association with Rock hyrax, *Procavia capensis* (Pallas) (Procaviidae), also probably breeding in droppings (Barraclough 1994; Deeming 1997). Undescribed, or at least unidentified, *Meoneura* species were reported by: Oldroyd (1958), from a penguin rookery on Gough Is. in the South Atlantic; Braak (1986) from mammalian carcasses; Deeming (1976) from the stomach of a Ruff, *Philomachus pugnax* Rafinesque (Scolopacidae), along the western margins of Lake Chad, Nigeria; and Deeming (1997) from African bush elephant dung in Nigeria. The *Meoneura* collected from African bush elephant dung was later identified as *M. palaestinensis* Hennig, 1937 (Stuke, unpubl.).

Due to their small size and restricted habitat preferences, carnids are rarely observed in the wild and hardly any ecological associations are known. Adult *Hemeromyia* and *Meoneura* are recorded as visiting flowers, including the botanical families Apiaceae, Asteraceae and Rosaceae (Carles-Tolrá 1992, 2008; Roháček 1996), but no species-specific preferences have been reported. The frequently cited association of Carnidae with fungi may not be the only saprophytic association. Chandler (1998, 2002), for example, observed male aggregations of *M. neottiophila* Collin, 1930, on two species of fungi and hypothesised that flies may be using the fungal caps merely as courtship display sites. *Carnus* species are recorded from birds' nests, where the larvae develop and *C. hemapterus* Nitzsch, 1818, is recorded in association with a wide range of avian hosts (e.g., Capelle & Whitworth 1973; Grimaldi 1997; Heddergott 2005; Walter & Hudde 1987). At least two species of mites in the family Microtrombidiidae (Acari) occur as parasites on *Meoneura* (Fain & Grootaert 1994).

Valera *et al*. (2006*b*) noted prolonged multi-year puparial diapause of *Hemeromyia*. Stuke & Tago (2017) described a winter active *Meoneura* species from Japan and some species described from Israel are largely active in the moderately warm and more humid autumn and winter months (Stuke & Freidberg 2017). At least some species are polyvoltine and may be active in suitable environments year-round.

There are few published descriptions of the immature stages of Carnidae, upon which these notes and the below identification key are based. De Meijere (1912) and Valera & Zídková (2012) described the egg of *Carnus hemapterus*. Descriptions of larvae and puparia for extralimital species were only provided by: Capelle & Whitworth (1973) and de Meijere (1912), for *C. hemapterus*; Engel (1930), for a *Meoneura* sp.; Grimaldi (1997), for *C. occidentalis* Grimaldi, 1997; Papp (1998: 213), for *C. hemapterus* and *M. neottiophila*; Rotheray (2012), for *C. hemapterus*, *M. lamellata* Collin, 1930 and *M. neottiophila*; and by Valera *et al*. (2018), for *C. hemapterus*, *Hemeromyia anthracina* Collin, 1949 and *H. longirostris* Carles-Tolrá, 1992.

Economic significance

No economic impact of Carnidae has been reported to date. Potential impact has been assumed several times, but no evidence for these assumptions is presented. Iwasa *et al*. (2000, 2008) reported one case of *C. hemapterus* causing human dermatitis. Abd El-Halim *et al*. (2004) pointed out the potential for *Meoneura* to transmit pathogens to human food in Egyptian markets, as the species develops in feces and other animal dung. Engel (1930) and Sabrosky (1959) recorded large numbers of *M. obscurella* (Fallén, 1823) larvae infesting stored grain, feeds and tobacco, but it is likely that these products were damp and probably infested by fungi in this case, as there are no other records of dried plant products being attacked by the family.

The only observations concerning an ecological impact of Carnidae are from species associated with nestling birds. Adults of *Carnus* feed on blood and the larvae are probably saprophagous within nests (Nöller 1920). Liker *et al*. (2001) summarised the effect of *Carnus* on its hosts and could only find one investigation where a fitness loss due to *Carnus* has been recorded: Kirkpatrik & Colvin (1989) recorded that owls had higher rates of protozoan blood infections associated with higher infestation rates of *C. hemapterus* and Iwasa *et al*. (2014) noted that the study of species of *Carnus* in all regions as vectors of avian blood pathogens was merited. Robitzky (2010) observed that Peregrine falcons, *Falco peregrinus* Tunstall (Falconidae), abandoned breeding sites following heavy infection with *Carnus*. Podofillini *et al*. (2018), however, noted that dirty nest boxes containing *C. hemapterus* were actually preferred by Lesser kestrel, *Falco naumanni* Fleischer (Falconidae), hatching success was higher than in clean boxes and there was no statistical difference in the growth rates of hatchlings in boxes infested with *C. hemapterus*. Thus, the ecological impact of this parasite is questionable at best.

Classification

Carnidae were originally considered as the subfamily Carninae, within the family Milichiidae by numerous authors. Griffiths (1972: 235) and Hennig (1972) were the first to definitively discuss relationships of the Carnidae. Interpretations of relationships between Carnidae and other families have varied widely. Griffiths (1972: 235), including Carnidae with non-Afrotropical Acartophthalmidae, Chloropidae and Milichiidae in a Chloropidae family-group. McAlpine (1989: 1468) proposed including the families Australimyzidae, Braulidae, Canacidae (including Tethinidae), Carnidae, Chloropidae, Cryptochetidae, Milichiidae and Risidae as the superfamily Carnoidea. Wiegmann & Yeates (2017: 255) and Wiegmann *et al*. (2011) recovered Carnidae in an unnamed clade, with Agromyzidae, Odiniidae, Periscelididae and Sphaeroceridae.

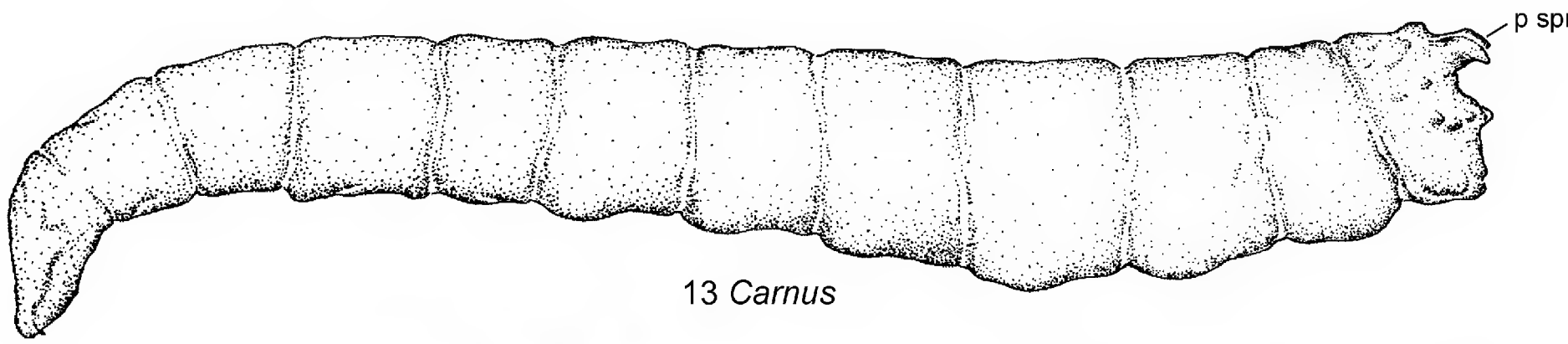
The phylogeny within the family is detailed and convincingly elaborated on by Buck (2006), Buck & Marshall (2007) and Grimaldi (1997), based on cladistic analyses of morphological characters.

Three fossil species are known, two species of *Meoneura* from Baltic and Dominican amber and the monotypic genus *Meoneurites* Hennig, described from Baltic amber. Fossil *Meoneurites* is sister-group to the Neotropical genus *Neomeoneurites* Hennig, forming an early branching clade to the remaining four extant Carnidae genera (((*Carnus* + *Meoneura*) + *Enigmocarnus* Buck) + *Hemeromyia*).

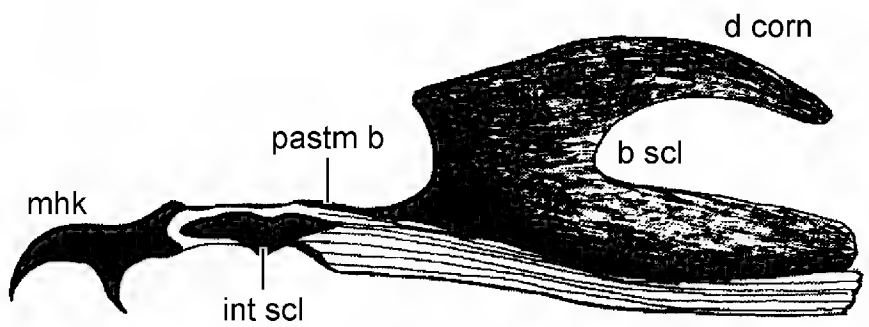
Identification

There are currently no comprehensive species-level identification keys to the Afrotropical Carnidae fauna. Generic level identification keys for the world fauna were provided by Brake (2011), Buck & Marshall (2007) and Hennig (1972), and for the Afrotropical fauna specifically, by Barraclough (1994). By far the most elaborated diagnoses are, however, provided by Buck (2006) and Grimaldi (1997) and the below identification key to adults is largely based on their descriptions. Specific identifications of all endemic Afrotropical Carnidae can only be achieved by reference to the original descriptions of Barraclough (1994) and Deeming (1976, 1997). The few Afrotropical *Meoneura* species with a wider distribution are all included in the identification keys provided by Stuke & Freidberg (2017). Specific identifications of larvae are not possible at this time, but third-instar larvae and puparia can be identified to genus-level, using the below identification key, which is based on Papp (1998: 215), amended according to Valera *et al*. (2018).

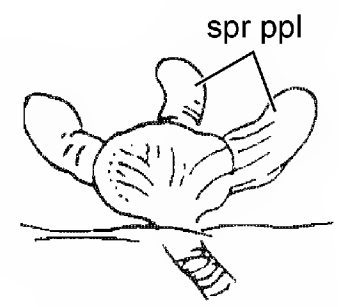
Although Carnidae are occasionally sampled in Malaise traps in the Afrotropics, they are best collected at their normal larval breeding sites, such as hyrax abodes, birds' nests and the runs, droppings and nests of small mammals. One effective method is to rear adults directly from the larval substrate or breeding medium. Pan and Malaise trapping, especially if baited with dung or carrion, is another highly effective technique for sampling carnids, especially the genus *Meoneura*. Carnidae are best micropinned in the field for later double-mounting (see Chapter 2).



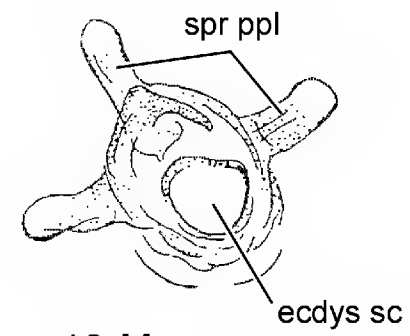
13 *Carnus*



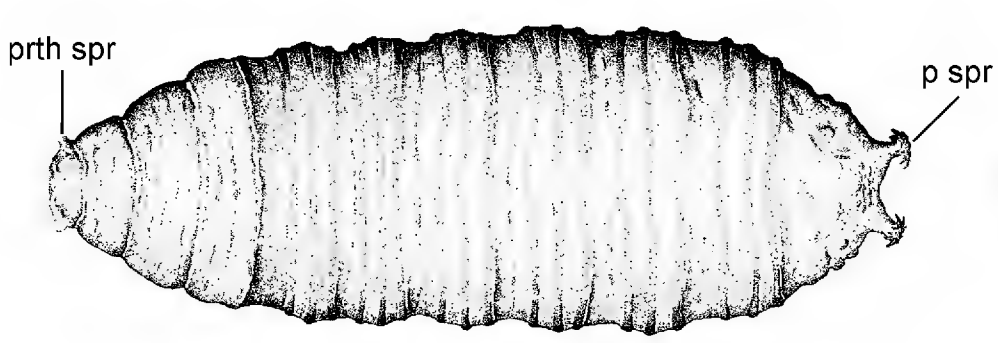
14 *Carnus*



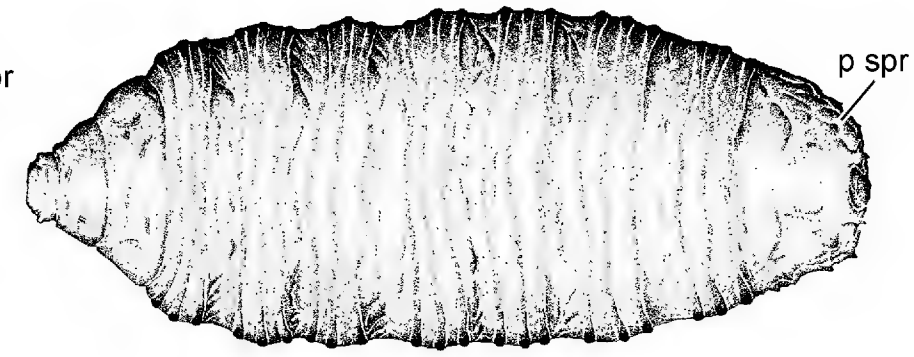
15 *Meoneura*



16 *Meoneura*



17 *Carnus*



18 *Meoneura*

Figs 93.13–18. Immature stages of Carnidae: (13) larval habitus of *Carnus hemapterus* Nitzsch, lateral view (non-Afrotropical); (14) same, cephaloskeleton, lateral view; (15) prothoracic spiracle of *Meoneura obscurella* (Fallén), dorsal view (non-Afrotropical); (16) same, posterior spiracle, caudal view; (17) puparial habitus of *C. hemapterus*, dorsal view; (18) same, *M. neottiophila* Collin, dorsal view (non-Afrotropical). Figs 13, 14, 17, 18 (Papp 1998, figs 10, 13–15), Figs 15, 16 (after Engel 1930, figs 4, 5).

Abbreviations: b scl – basal sclerite; d corn – dorsal cornu; ecdys sc – ecdysial scar; int scl – intermediate sclerite; mhk – mouthhook; p spr – posterior spiracle; pastm b – parastomal bar; prth spr – prothoracic spiracle; spr ppl – spiracular papillae; v corn – ventral cornu.

Keys to genera of Afrotropical Carnidae

Adults

1. Wing usually broken-off, leaving short stub (Figs 1, 8), or if wing complete, then without discal medial crossvein (*dm–m*) (Fig. 5); abdominal membrane with numerous long, dense setulae (Figs 1, 8); female abdominal sternites lost (Fig. 1); male terminalia with distiphallus short, without vestiture . . . . . *Carnus* Nitzsch

– Wing complete, with discal medial crossvein (*dm–m*) (e.g., Figs 6, 7); abdominal membrane with scattered, short setulae; female tergites and sternites normally developed; male terminalia with distiphallus long, coiled, with distinct vestiture (e.g., Figs 9, 10) 2

2. Wing (Fig. 6), with costal vein (*C*) clearly extending to vein M_1; vein M_1 well-developed, distinct beyond discal medial crossvein (*dm–m*); crossvein *dm–m* much longer than radial–medial crossvein (*r–m*), distance along vein M_1 from crossveins *r–m* to *dm–m* at least 3 × length of *r–m*; anterior cubital cell (*cua*) closed; vein *CuA+CuP* strongly developed; subcostal vein (*Sc*) normally developed; mouthparts with labium not enlarged to bulbous and longer than rest of proboscis; male tergite 6 reduced; female terminalia with cercus short, not longer than broad . . . . . *Hemeromyia* Coquillett

– Wing (Fig. 7), with costal vein (*C*) extending to vein R_{4+5}; vein M_1 weakly developed, indistinct beyond discal medial crossvein (*dm–m*); *dm–m* roughly equal in length to radial medial–crossvein (*r–m*), with distance between veins along vein M_1 almost equal to length of crossveins *r–m* to *dm–m*; anterior cubital cell (*cua*) open; vein *CuA+CuP* weak or absent; subcostal vein (*Sc*) incomplete or absent; mouthparts with labium enlarged to bulbous, longer than rest of proboscis; male tergite 6 absent; female cercus longer than broad (Figs 11, 12) . . . . . *Meoneura* Rondani

Larvae and puparia

1. Posterior spiracles without protuberances. . . . . *Hemeromyia* Coquillett

– Posterior spiracles with 3 protuberances (e.g., Fig. 16) 2

2. Larval prothoracic spiracle with 5–7 spiracular papillae; puparial posterior spiracles situated caudally (Fig. 17) . . . . . *Carnus* Nitzsch

– Larval prothoracic spiracle with 3 spiracular papillae (Fig. 15); puparial posterior spiracles situated dorsally (Fig. 18) . . . . . *Meoneura* Rondani

Synopsis of the fauna

Globally the family Carnidae currently comprises 127 extant described species in five genera. Although the family was thought to be largely Holarctic in distribution, it is probable that this under-collected family is widely distributed in the Afrotropics and that in every genus undescribed species await discovery and description. Carnidae are rarely collected in Malaise traps and other passive sampling methods, probably due to their highly specialised biology and niche preferences, so making an assessment of the likely number of undescribed species in the region is problematic.

***Carnus* Nitzsch.** A genus of five described species, occurring in the Nearctic, Neotropical, Oriental and Palaearctic Regions. There is currently only one published record of *Carnus* from the Afrotropical Region: de Coninck (1986: 49) found an unidentified specimen in Democratic Republic of Congo, on nestlings of the Brown-hooded kingfisher, *Halcyon albiventris* (Scopoli) (Alcedinidae), which is widespread throughout Southern Africa. El-Hawagry *et al*. (2016) reported *C. hemapterus* from Saudi Arabia, in the adjacent Palaearctic Region.

***Hemeromyia* Coquillett.** A genus of nine described and additional undescribed species, occurring in the Afrotropical, Nearctic and Palaearctic Regions. The only Afrotropical species described to date, *H. australis* Barraclough, 1994, has only been reported from two localities in Namibia (Barraclough 1994; Papp 2013). The larval stages are associated with nestling birds, but the immature stages remain unknown.

***Meoneura* Rondani.** The largest genus of Carnidae with 109 extant species, occurring in all zoogeographical regions, except the Australasian/Oceanian Region and Antarctica. Seven species are recorded from the Afrotropics: *M. prima* (Becker, 1903), widely distributed throughout the Afrotropical Region and Holarctic Realm; *M. palaestinensis*, widely distributed from Cabo Verde, North Africa, the Arabian Peninsula to Ethiopia, as far north as Turkey; and *M. biseta* Deeming, 1976, from Nigeria and Yemen. The remaining four species are endemic to sub-Saharan Africa and only the type material is known: *M. australis*, described from South Africa; *M. nigeriensis* Deeming, 1976 and *M. scutellata* Deeming, 1976, both described from Nigeria; and *M. nigrohalterata*, described from Namibia.

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CANACIDAE 94

(Beach Flies, Surf Flies and Surge Flies)

Lorenzo Munari and Wayne N. Mathis

Fig. 94.1. Female of *Horaismoptera vulpina* Hendel (Tanzania) (Photograph © S.A. Marshall).

Diagnosis

The family Canacidae *sensu lato* (Fig. 1) is distinguished from other families of Carnoidea by the following combination of characters: primarily occurring in saline habitats (secondarily in freshwater habitats); minute to small-sized acalyptrate flies (body length: 0.91–5.0 mm), with whitish or pale yellow to dark brown body and pale yellow to blackish legs.

Head (Figs 2–14), with postocellar (= postvertical) setae usually developed (absent in *Tethina lusitanica* Munari, Almeida & Andrade, 2009, absent or reduced in some Canacinae); posterior fronto-orbital seta lateroclinate; vibrissa weakly differentiated (except in *Dasyrhicnoessa* Hendel); antennal arista dorsal; face sometimes characterised by shiny protuberance just above vibrissal socket (*Tethina* Haliday *in* Curtis and *Pseudorhicnoessa* Malloch), or nearby (*Afrotethina* Munari and *Horaismoptera* Hendel); face strongly depressed and short (*Dasyrhicnoessa* and Horaismopterinae), or with median carina (*Tethina*), or distinctly convex (Canacinae); gena usually bare, except for ventral, or nearly ventral, row of setae (subvibrissal setae), or even with a few dorsoclinate (= anaclinate), strong setae (Canacinae); buccal parts generally strongly sclerotised in Canacinae.

Thorax with precoxal bridge developed; prescutellar acrostichal setae usually developed; presutural dorsocentral setae differentiated; anepisternum with 2–3 developed posterior setae, also bearing dorsoclinate seta at posterodorsal corner; 1 katepisternal seta usually present; proepisternal seta developed. Wing (Figs 15–17) generally hyaline, bearing fine, dense microtrichia; subcostal vein (*Sc*) usually weakened apically, close to vein R_1; vein *CuA+CuP* short (except in the sub-Antarctic genus *Apetaenus* Eaton and in *Horaismoptera* (Fig. 15), having this vein extended to wing margin as obvious fold); vein A_1 long, present as a fold.

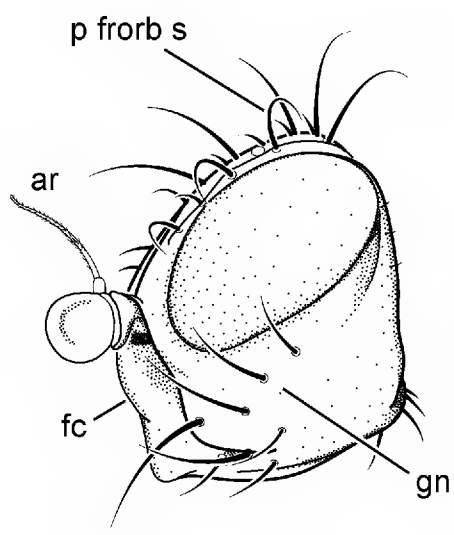
Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2021. Manual of Afrotropical Diptera. Volume 3. Brachycera—Cyclorrhapha, excluding Calyptratae. *Suricata* 8. South African National Biodiversity Institute, Pretoria; pp. 2003–2014.

Abdomen (Figs 24–26), with pregenital sclerites of male short and fused; male tergite 6 fused with sternite 8, forming usually symmetrical pregenital sclerite behind tergite 5; sternites 6 and 7 and tergites 7 and 8 indistinguishable, these tergites forming syntergosternite 7 + 8 (Fig. 24); postgonites firmly connected laterally to base of phallapodeme, or medially to it, distinctly anterior to basiphallus; hypandrium forming sheath, or phallic mantle, around postgonite and basiphallus; epandrium bearing 1–2 pairs of surstyli ventrally, sometimes anterior surstylus lacking (Canacinae and *Tethina*); posterior surstylus partially articulated or fused with epandrium; mediobasal corner of surstylus connected to broad bacilliform sclerite; cercus very short to exceptionally developed (Horaismopterinae); postabdomen of female (Figs 25, 26) more or less retracted telescopically; 2 sclerotised spermathecae present, variable in shape, with narrower cylindrical extension into spermathecal duct; cercus sub-cylindrical to tapered distally, sometimes bearing stout to pointed, spine-like setae (Figs 22, 23).

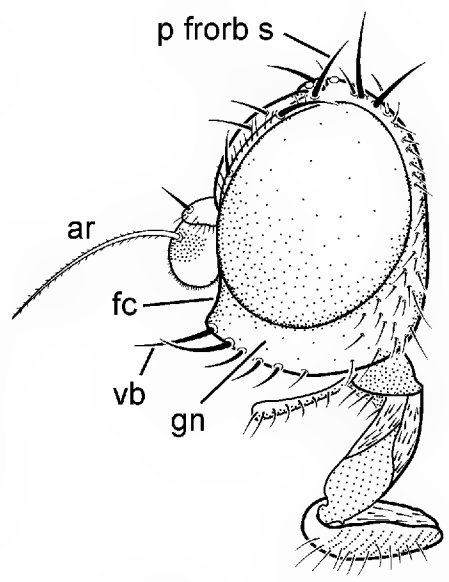
Adult Canacidae in the subfamily Canacinae may be superficially confused with some Ephydridae (see Chapter 100), while small species of the subfamilies Tethininae and Zaleinae may be misinterpreted as Chyromyidae (see Chapter 97) or Chloropidae (see Chapter 96). The subfamilies Horaismopterinae and Pelomyiinae are strongly characterised, without any possibility of confusion with other Diptera. The somewhat numerous and highly diversified diagnostic characters of the Canacidae in general can be carefully considered by using the Key to the families – adults presented in Chapter 12.

Biology and immature stages

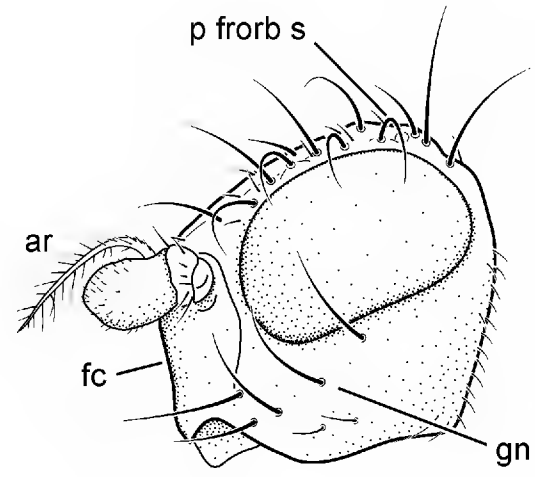
The biology and immature stages (Figs 27–30) of the family are poorly known and the published record on the natural history of the Afrotropical fauna is virtually non-existent. Habitats where Canacidae are found are sometimes characterised by a surfeit of individuals and a relative paucity of species.



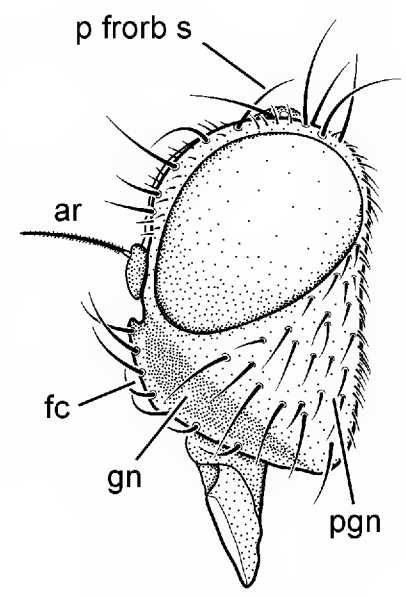
2 *Canace*



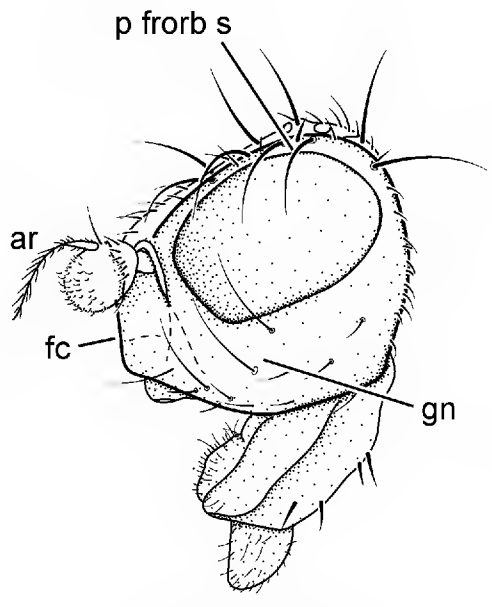
3 *Dasyrhicnoessa*



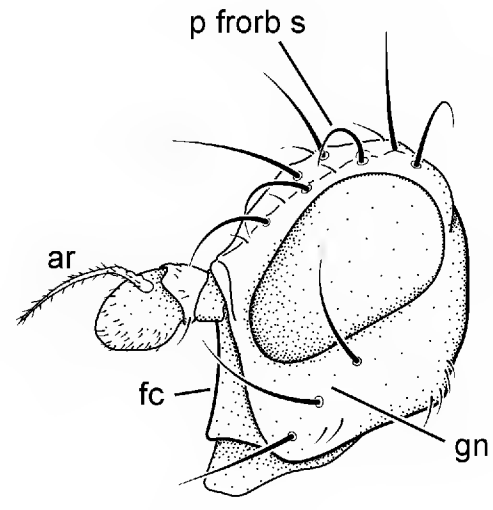
4 *Dynomiella*



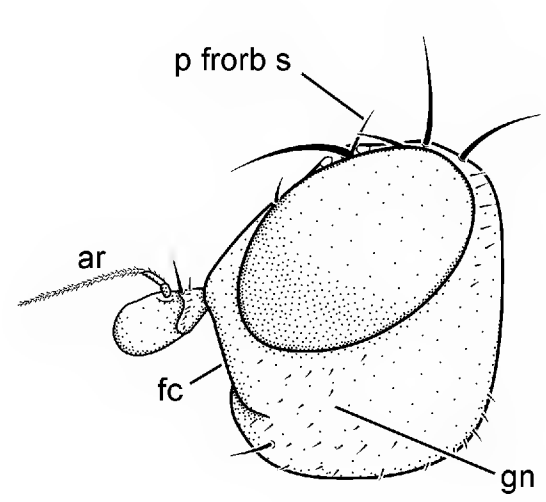
5 *Horaismoptera*



6 *Isocanace*



7 *Nocticanace*



8 *Pelomyiella*

Figs 94.2–8. Heads of Canacidae (lateral views): (2) *Canace nasica* (Haliday); (3) *Dasyrhicnoessa insularis* (Aldrich); (4) *Dynomiella stuckenbergi* (Wirth); (5) *Horaismoptera vulpina* Hendel; (6) *Isocanace flava* (Canzoneri & Meneghini); (7) *Nocticanace flavipalpis* Mathis & Wirth; (8) *Pelomyiella mallochi* (Sturtevant). Fig. 2 (after Mathis 1982*b*, fig. 4), Fig. 3 (after Hardy & Delfinado 1980, fig. 151a), Figs 4, 7 (after Mathis & Wirth 1979, figs 6, 8), Fig. 5 (after Munari 1998, fig. 19.2), Fig. 6 (after Mathis 1999, fig. 27).

Abbreviations: ar – arista; fc – face; gn – gena; p frorb s – posterior fronto-orbital seta; pgn – postgena; vb – vibrissa.

Globally, most taxa of the subfamily Canacinae occur in intertidal and supralittoral habitats. An exception is *Procanace grisescens* Hendel, 1913, a species occurring in the Afrotropical and Oriental Regions in freshwater environments (usually mountain streams). Although feeding habits are poorly known, larvae and adults are probably grazers on algae, or are saprophytic. Larvae of *Canace salonitana* Strobl, 1900, have been collected and reared and occur on protected sides of large rocks along the coast of the Mediterranean Sea in Israel (Mathis 1982*b*). The rocks concerned were covered with algae to varying degrees, which is probably the food source for both larvae and adults.

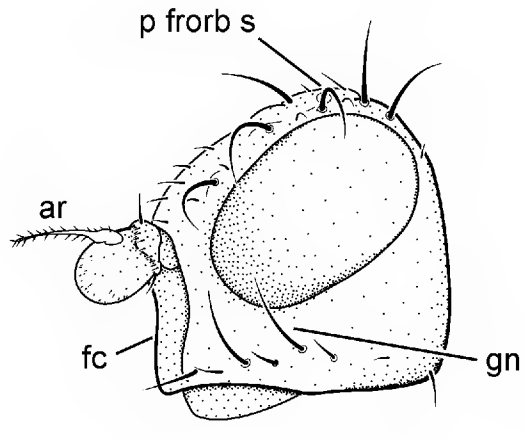
Flies of the subfamily Horaismopterinae inhabit oceanic seashores. The biology of the immature stages remains unknown.

Tethininae are mostly halobionts and, in many cases, thalassobiont flies, occurring in coastal marine habitats. Adults of thalassobiont species are commonly found in the intertidal and supralittoral zones, wrack heaps (usually brown algae that are most abundant along temperate seashores bathed by cold currents), salt marshes, dune vegetation, lagoon-litoriparian zones, mangroves (particularly species of *Dasyrhicnoessa*) and on saline soils, or bare sand. Various species of the genus *Tethina* also inhabit desert oases and other inland environments sometimes hundreds of kilometres from sea coasts (Beschovski & Nartshuk 1997; Munari 2005). The biology, including the immature stages of the subfamily, is poorly known and is not germane to species inhabiting the Afrotropical Region. Adults of Tethininae have been observed, often in large numbers, on carcasses of marine animals or fish on beaches (W.N. Mathis, pers. obs.; Munari 2004 (see entry for *Thitena cadaverina* Munari, 2004).

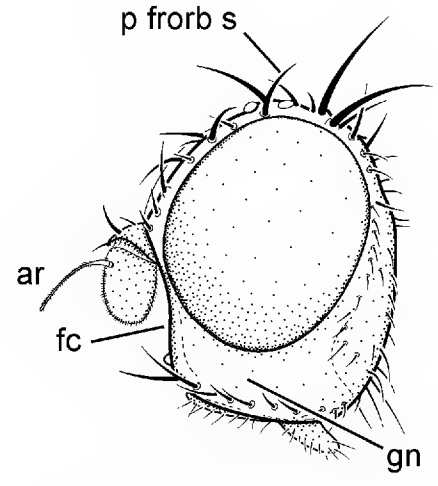
As far as is known, only seven parasites of Canacidae are recorded in the literature (Munari & Mathis 2010; Roth & Brown 1976: 129). In the Afrotropical Region, Rossi (1988) and Rossi & Cesari Rossi (1979) described two new species of Laboulbeniales (Ascomycetes) parasitic on *Pseudorhicnoessa rattii* Munari, 1981 (Tethininae) from Seychelles and on *Canace nasica* (Haliday *in* Curtis, 1837) (Canacinae) from Senegal, respectively.

Economic significance

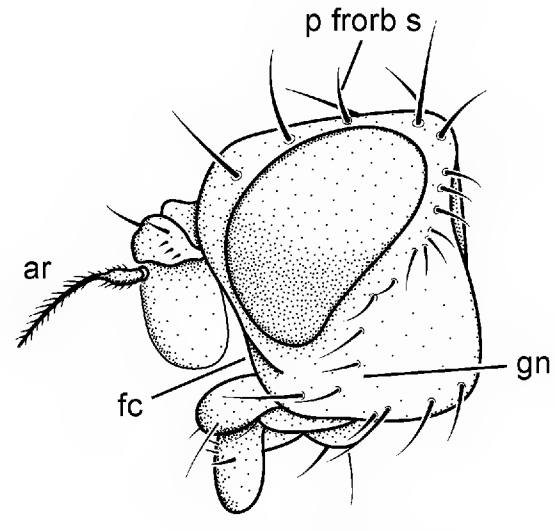
The canacid flies apparently have no significant economical or medical importance.



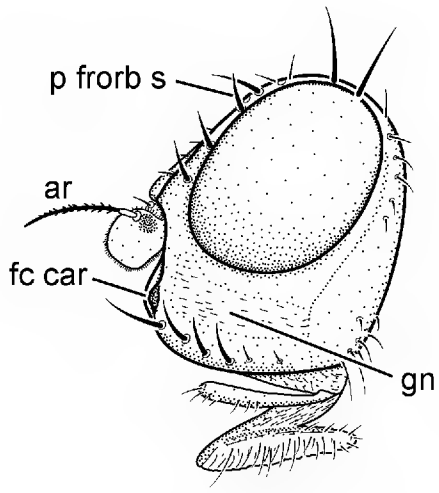
9 *Procanace*



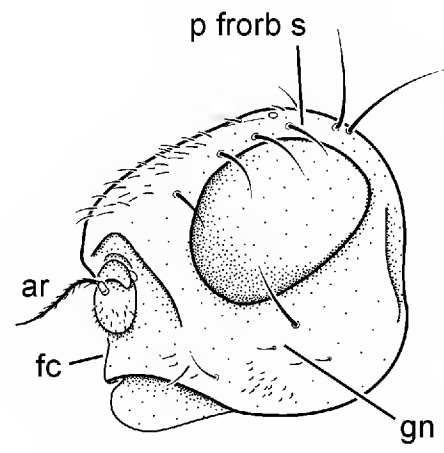
10 *Pseudorhicnoessa*



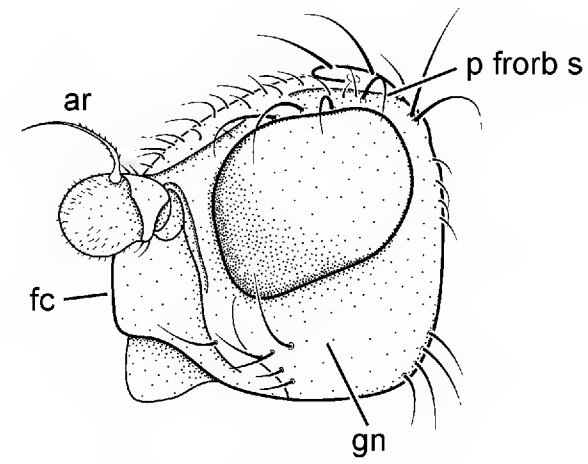
11 *Suffomyia*



12 *Tethina*



13 *Trichocanace*



14 *Xanthocanace*

Figs 94.9–14. Heads of Canacidae (lateral views): (9) *Procanace pauliani* Mathis & Wirth; (10) *Pseudorhicnoessa rattii* Munari; (11) *Suffomyia scutellaris* Freidberg; (12) *Tethina pallipes* (Loew); (13) *Trichocanace sinensis* Wirth; (14) *Xanthocanace kaplanorum* Mathis & Freidberg. Fig. 9 (after Mathis & Wirth 1979, fig. 10), Fig. 11 (after Freidberg 1995, fig. 1), Fig. 12 (after Munari 2011, fig. 29), Fig. 14 (after Mathis & Freidberg 1982, fig. 1).

Abbreviations: ar – arista; fc – face; fc car – facial carina; gn – gena; p frorb s – posterior fronto-orbital.

Classification

The concept of Canacidae adopted here, comprises what were previously considered two families, *i.e.*, the Canacidae and Tethinidae. At the family-level, McAlpine (1989: 1472) identified five synapomorphies that link the Canacidae *sensu stricto* with Tethinidae and noted that "... there are clear indications of a sister-group relationship between them ... and may even indicate that they are subgroups of a single family". Other authors (*e.g.*, Freidberg 1995; Griffiths 1972: 258; Hennig 1958; McAlpine 1982), have also suggested a relationship between these two families. According to McAlpine's (1989: 1469) cladogram, which included an analysis of 25 character states for the families Canacidae *sensu stricto* and Tethinidae, the Canacidae *sensu lato*, together with Australimyzidae (non-Afrotropical), Braulidae, Carnidae, Chloropidae (including Minidae and Siphonellopsidae), Cryptochetidae, Milichiidae and Risidae (non-Afrotropical) comprise the superfamily Carnoidea (= Chloropoidea). Of the 25 character states McAlpine considered, five were determined to be synapomorphies that establish the monophyly of the Canacidae/Tethinidae lineage.

More recently, Buck (2006) and McAlpine (2007) provided rather compelling character evidence, substantiating that these two families are closely associated, and more specifically, that the Canacidae *sensu stricto* are an included lineage within the Tethinidae. Thus, not to include the Canacidae within the Tethinidae would render the Tethinidae a paraphyletic family. Buck (2006) cited nine autapomorphies that corroborate the monophyly of the family Canacidae *sensu lato* (the family-group name Canacidae antedates Tethinidae). These autapomorphies are: (1) precoxal bridge present; (2) anepisternum with developed, dorsoclinate seta in posterodorsal corner; (3) vein A_1 long, present as a fold; (4) male sternite 6 reduced and divided medially; (5) male tergite 6 fused with sternite 8, forming a symmetrical pregenital sclerite; (6) male sternite 7 lacking; (7) postgonites firmly connected laterally to base of phallapodeme, distinctly anterior to basiphallus; (8) hypandrium forming a sheath, or phallic mantle, around the postgonite and basiphallus; (9) halobiontic and halophilic in habitat preference [secondarily in freshwater habitats]. Buck (2006) further suggested that the sister-group to Canacidae *sensu stricto* could likely be the sub-Antarctic subfamily Apetaeninae, not the Zaleinae and provided four character states as evidence of this relationship: (1) antennae broadly separated, inserted on more or less protuberant facial tubercles; (2) clypeus distinctly enlarged and produced anteriorly; (3) prementum distinctly emarginated apically; and (4) tentorial arms of head enormously developed and strongly sclerotised. It should be noted, however, that D.K. McAlpine (pers. comm. 2010) disagrees to a large extent with most of Buck's proposed synapomorphies for Canacidae *sensu lato* (see above).

Since McAlpine's (2007) reassessment of Canacidae/Tethinidae, the former subfamilies of the Canacidae *sensu stricto* were automatically downgraded at the tribe level, while Canacidae *sensu stricto* is now regarded as the nominal subfamily of Canacidae *sensu lato*. As far as the former family Tethinidae is concerned, McAlpine (2007) maintained the same subfamilies as traditionally accepted in the modern literature, contextually downgrading the family-group name Tethinidae to a junior synonym of Canacidae *sensu lato*. Thus, according to McAlpine, the Canacidae now comprise the following subfamilies: Apetaeninae, Canacinae (including Nocticanacinae), Horaismopterinae, Pelomyiinae, Tethininae and Zaleinae. In the most recent world catalogue of the family, six subfamilies were recognised (Munari & Mathis 2010).

No species of fossil Canacidae have been described (Evenhuis 1994: 476), although undetermined specimens of Tethininae have been recorded from the Oligocene/Miocene amber of Chiapas, Mexico (Hurd *et al*. 1962; Poinar 1992). These specimens have not been examined by a specialist to verify their status.

Identification

The following publications contain keys, illustrations and/or diagnoses that will facilitate identification of many Afrotropical species (checklists or catalogues are also included). These publications are annotated with a capital C (= Canacidae *sensu stricto*), T (= Tethinidae), or both, as until recently (McAlpine 2007) the genera and species dealt with were included in the two former families, Canacidae *sensu stricto* and Tethinidae. The publications are as follows: Wirth [C] (1956, 1960, South African fauna); Canzoneri & Meneghini [C] (1969, Afrotropical fauna); Vanschuytbroeck [T] (1976, fauna of St. Helena Is.); Mathis & Wirth [C] (1979, fauna of Madagascar); Cogan [C, T] (1980*a*, *b*, catalogue); Munari [T] (1988, fauna of Seychelles; 1990, fauna of Aldabra Is.; 1994, checklist of Afrotropical fauna; [C-T] 2016, review of Arabian fauna); Mathis [C] (1988, fauna of Seychelles); Mathis & Freidberg [C] (1991, review of the Afrotropical Canacini and Nocticanacini); Kirk-Spriggs *et al*. [C, T] (2001, fauna of Namibia and South Africa, keys to species); Munari *et al*. [T] (2020, fauna of the Mascarene Is.); Munari *et al*. [C] (2021, fauna of the Mascarene Is.). Canacidae are best micro-pinned in the field for later double-mounting (see Chapter 2).

Key to genera of Afrotropical Canacidae

1. Head with gena bare (*e.g.*, Figs 3, 10, 12) (gena not to be confused with occasionally wide, setulose postgena, *e.g.*, *Horaismoptera*, Fig. 5), or with a few large dorsoclinate setae; face (at least in ventral part), almost vertical, with vibrissal angle not receded; if face in profile convex ventrally (in *Horaismoptera*), then costal wing vein (C) with widely spaced, long spines (*e.g.*, Fig. 15) 2

– Head with gena bearing numerous very pale, minute setulae (in Afrotropical species, Fig. 8) to black, minute setulae; face in profile convex ventrally, with vibrissal angle distinctly receded; costal wing vein (C) with short setulae only (PELOMYIINAE) . . . . . *Pelomyiella* Hendel

2. Head with 3 major lateroclinate fronto-orbital setae, foremost near level of ptilinal fissure, in addition to medial series of 3 or more proclinate/inclinate shorter setae or setulae (*e.g.*, Figs 3, 10, 12); 3–4

proclinate/inclinate interfrontal setae arranged in 2 distinct series; pair of convergent, often widely spaced, postocellar setae present; if absent, then wing with distinct, black maculae (in the Palaearctic species *Tethina lusitanica*); costal vein (C) along marginal cell with continuous series of closely placed, short, black, anterior spinules, but without series of longer, widely spaced spines; discal medial (*dm*) and basal medial (*bm*) cells separate; anterior cubital (*cua*) cell closed; vein *CuA+CuP* not extending distinctly beyond anterior cubital cell, even as sharp fold in membrane (TETHININAE) 3

– Head with both fronto-orbital setae and interfrontal chaetotaxy not as above; if lateroclinate fronto-orbital setae present, then clypeus more or less obviously protruding and face prominent, extensively visible in profile; if biseriate interfrontal setae present, then either convergent postocellar setae absent, or cell *cua* open distally; other characters variable 6

3. Compound eye appearing bare, without ommatrichia; shiny tubercle above vibrissal angle invariably present (Fig. 12); mid and hind tibiae evenly setulose, lacking anterodorsal and posterodorsal setae (except for the Australasian species *Tethina hirsuta* Munari, 2000); scutellar disc bare; epandrium of male terminalia with 1 pair of surstyli, partially fused with epandrium (Fig. 24) . . . . . *Tethina* Haliday

– Compound eye micro-pubescent, densely clothed in pale ommatrichia; shiny tubercle above vibrissal angle variable; mid and hind tibiae with or without strong anterodorsal and posterodorsal setae; scutellar disc bearing short setulae, if bare, then lacking shiny tubercle above vibrissal socket; epandrium of male terminalia with 2 pairs of surstyli 4

4. Head with true vibrissal seta; without shiny tubercle or fold above vibrissal angle (Fig. 3); scutellar disc bare, except for marginal setae; anterior surstylus of male terminalia varying in shape, but never hook-like curved. . . . . *Dasyrhicnoessa* Hendel

– Head without true vibrissal seta, sometimes substituted by foremost inclinate subvibrissal seta, simulating true vibrissal seta; with shiny tubercle laterad to ventral part of face, sometimes barely visible as shiny fold bordering vibrissal socket dorsally (e.g., Fig. 18) (*Afrotethina*), in some instances present as subshiny bulge laterad to ventral part of face, just above vibrissal angle (Fig. 10) (*Pseudorhicnoessa*); scutellar disc clothed in more or less scattered setulae, in addition to marginal setae; shape of anterior surstylus of male terminalia variable 5

5. Mid and hind tibiae evenly setulose, lacking anterodorsal and posterodorsal setae (Fig. 18); all femora and tibiae unicolourous; anterior surstylus of male terminalia invariably curved, hook-like . . . . . *Afrotethina* Munari

– Mid and hind tibiae bearing strong anterodorsal and posterodorsal setae; at least hind femur and tibia with apical brown ring (Fig. 20); anterior surstylus of male terminalia not shaped as above. . . . . *Pseudorhicnoessa* Malloch

6. Wing cell *cua* open distally; alula strongly reduced; tiny flies (body length of the Afrotropical species: 1.3–1.6 mm) (ZALEINAE). . . . . *Suffomyia* Freidberg

– Wing cell *cua* closed; alula well-developed; generally distinctly larger flies (body length: 1.6–5 mm) 7

7. Head with frons with several proclinate setulae arranged in longitudinal, regular rows (Fig. 5); face (viewed in profile) convex ventrally with ventral part receded; vibrissal angle entirely absent (Fig. 5), the clypeus thus markedly displaced posteriorly; costal wing vein (C) bearing strong, spine-like setae in addition to the usual, short costal setulosity (Fig. 15) (HORAISMOPTERINAE). . . . . *Horaismoptera* Hendel

– Head with chaetotaxy of frons variable; face (viewed in profile) with at least ventral part almost vertical, not receded on ventral surface; vibrissal angle present (Fig. 9), the clypeus thus located approximately as far forward as anterior surface of head; costal wing vein (C) without spine-like setae (as in Fig. 16) (CANACINAE) 8

8. Head with 4 or more lateroclinate fronto-orbital setae; if 3 lateroclinate fronto-orbital setae present, then thorax generally without katepisternal seta; female terminalia with cercus with 1 large, apical spine-like seta and 1 (often barely discernible), smaller and weaker thick seta (Fig. 22), both usually acutely pointed (CANACINI) 9

– Head with 3 lateroclinate fronto-orbital setae; thorax with katepisternal seta; female terminalia with cercus with 2 subequally large, spine-like setae, 1 apical and 1 subapical, both rather blunt (NOCTICANACINI) 13

9. Head with 3 lateroclinate fronto-orbital setae (Fig. 2); thorax without katepisternal seta (CANACINA) . . . . . *Canace* Haliday

– Head with 4 or more lateroclinate fronto-orbital setae (e.g., Figs 4, 6, 13, 14); thorax sometimes with katepisternal seta (DYNOMIELLINA) 10

10. Thorax with katepisternal seta (sometimes pale) . . . . . *Isocanace* Mathis
– Thorax without katepisternal seta 11
11. Thorax with anterior notopleural seta; scutellum with 2 pairs of lateral setae 12
– Thorax without anterior notopleural seta; scutellum with I pair of lateral setae . . . . *Trichocanace* Wirth
12. Wing vein M_1 with last section slightly arcuate (Fig. 17); frontal vitta uniformly and densely setulose; head with 4–6 fronto-orbital setae; setae generally pale . . . . . *Xanthocanace* Hendel
– Wing vein M_1 with last section more or less straight, not distinctly arcuate; frontal vitta with bare areas, not densely setulose; head with 4 fronto-orbital setae; setae generally dark coloured . . . . . *Dynomiella* Giordani Soika
13. Head without interfrontal setae, although anterior ⅓ of frons occasionally with scattered setulae . . . . . *Procanace* Hendel
– Head with 1 or 2 interfrontal setae in addition to other setulae . . . . . *Nocticanace* Malloch

Synopsis of the fauna

Twenty-eight genera of Canacidae are currently recognised globally (Munari 2018*a*; Munari & Mathis 2010), 14 of which occur in the Afrotropical Region. Three hundred and twenty-one species are described worldwide, 66 of which occur in the Afrotropics. While the canacid flies from the eastern (including the oceanic islands) and southern coasts of sub-Saharan Africa are relatively well-known, very little is known about the canacid fauna of the western coast (Munari 2015) and no species has been recorded thus far from continental saline environments of Africa south of the Sahara (for North Africa, see Munari 2005). On Madagascar, 12 species belonging to seven genera of the subfamilies Canacinae, Horaismopterinae and Tethininae have been recorded (Munari & Mathis 2010), while 22 species belonging to seven genera (also including the subfamily Zaleinae) have been reported, or are exclusively known, from the Arabian states of Oman and United Arab Emirates. As is the case with many other families of Diptera, it can be predicted that a relatively large number of undescribed species are expected to be found throughout the Afrotropical Region. Kirk-Spriggs & Stuckenberg (2009: 184), for example, predicated that 63% of Afrotropical species of Diptera may be undescribed.

***Afrotethina* Munari** (Tethininae)**.** An endemic genus comprising eight species, one of which, *A. martinezi* Munari, 2005, is known exclusively from the Arabian Peninsula. Species of this genus are true thalassobionts, being exclusive to maritime habitats. Kirk-Spriggs *et al*. (2001) recorded three species of *Afrotethina* from the south-west African coast and discussed distribution patterns. The genus is mainly distinguished by the following combination of characters: presence of "shiny tubercle" laterad on face reduced to a small, subshiny fold bordering the vibrissal socket dorsally; disc of scutellum pubescent; and the anterior surstylus of male terminalia invariably curved, roughly hook-like. The biology and immature stages remain unknown. Munari (1991) provided an identification key to the six species then known and Kirk-Spriggs *et al*. (2001) to the species occurring in south-western Africa.

***Canace* Haliday *in* Curtis** (Canacinae: Canacini: Canacina)**.** An Old World genus; the six included species are only known from the maritime coasts of Europe, including the Mediterranean Sea and West Africa (north of the Equator) (Munari 2014*b*; Munari & Mathis 2010). Mathis & Freidberg (1991) last reviewed the three Afrotropical species, of which two, *C. rossii* Canzoneri, 1982 and *C. zvuv* Mathis & Freidberg, 1991, are apparently endemic to the West African coast. The third species, *C. nasica*, is found in the western Palaearctic Region, but also occurs in Senegal and Cabo Verde. *Canace* is distinguished by the following combination of characters: 3 lateroclinate fronto-orbital setae; 2–3 large, anaclinate genal setae; 4 (1 + 3) dorsocentral setae; acrostichal setulae generally evident in two rows; anepisternum usually with 2 large setae of subequal length along posterior margin, occasionally 3; and katepisternal seta lacking. The biology and immature stages are unknown. Mathis & Freidberg (1991) provided an identification key to Afrotropical species.

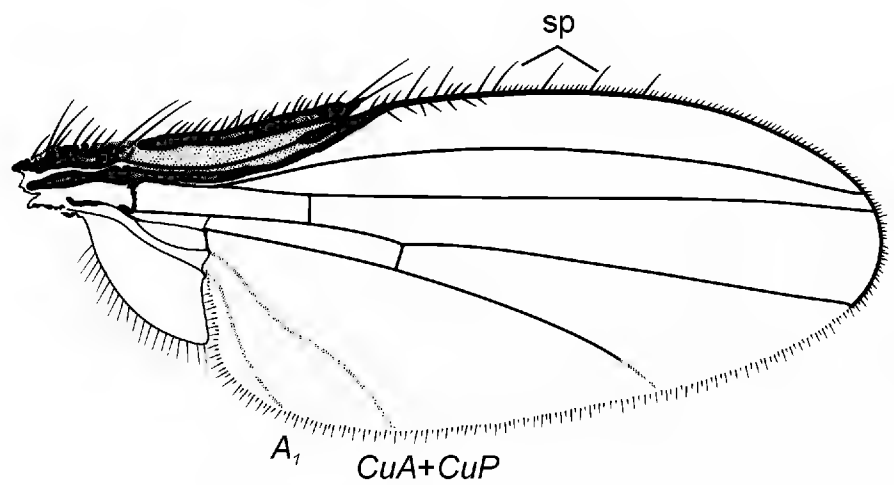
***Dasyrhicnoessa* Hendel** (Tethininae)**.** A pantropical genus of 29 described species (Munari 2014*a*, 2018*b*; Munari & Mathis 2010). Five species occur in the Afrotropics, namely: *D. adelpha* Munari, 2005, *D. ferruginea* (Lamb, 1914), *D. fulva* (Hendel, 1913), *D. insularis* (Aldrich, 1931) and *D. vockerothi* Hardy & Delfinado, 1980; perhaps introduced into the region through human activity. This genus is distinctive, especially from other genera in the subfamily Tethininae and is easily distinguished by the densely microtrichose eye; the prominent vibrissa; the face lacking a shiny tubercle above the vibrissal angle; and by both the anterior and posterior surstyli of the male terminalia. Species of *Dasyrhicnoessa* primarily inhabit mangrove swamps, although they also occur on beaches. The immature stages remain unknown. No identification key to Afrotropical species is currently available.

***Dynomiella* Giordani Soika** (Canacinae: Canacini: Dynomiellina)**.** A genus of five described species occurring in the Afrotropical and Australasian Regions. Four of the five species occur in Southern Africa, namely: South Africa and Namibia. The only remaining species, *D. australica* Mathis, 1996, is known from Australia (Tasmania Is.), which likewise has a temperate climate. *Dynomiella* is distinguished by the following combination of characters: setae in general dark coloured; 4 lateroclinate fronto-orbital setae; frontal vitta with bare areas, not densely setulose; anterior notopleural seta well-developed; katepisternal seta absent; and vein M_1 with last section more or less straight, not distinctly arcuate. The biology and immature stages remain unknown. Mathis (1982*a*) provided an identification key to known Afrotropical species.

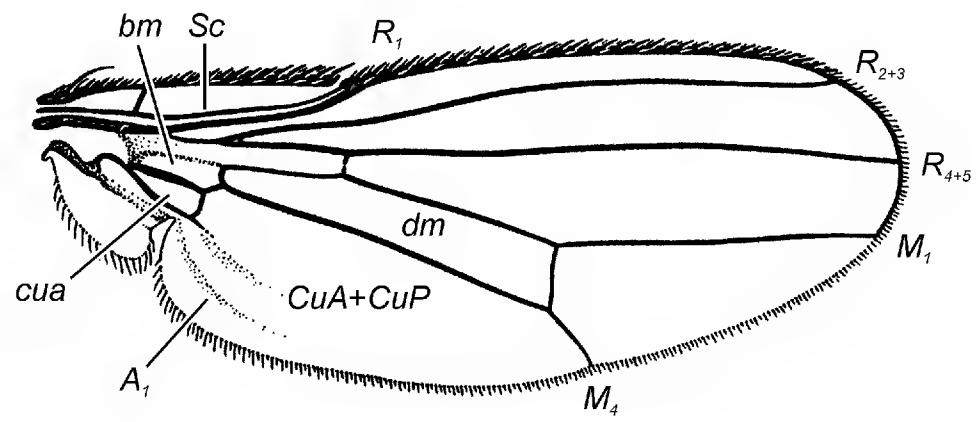
***Horaismoptera* Hendel** (Horaismopterinae)**.** The three included species are only known from the maritime coasts along the northern (Sri Lanka, *H. hennigi* Sabrosky, 1978) and western Indian Ocean, from the Red Sea and Persian Gulf southwards to South Africa, with some records from the Atlantic coast of Namibia (*H. microphthalma* (Bezzi, 1908)). A small genus, strongly characterised by the peculiar shape of the head in both anterior and lateral views and by the distinctive morphology of the male terminalia (Sabrosky 1978). The biology and immature stages remain unknown. Sabrosky's (1978) review of the genus provided an identification key to species, including schematic figures of the male terminalia and exhaustively discussed the family position of this highly derived genus, previously referred by some authors to five other families. Sabrosky proposed the new subfamily Horaismopterinae in that paper. Munari (2009) provided a complete distribution map for all species of the genus.

***Isocanace* Mathis** (Canacinae: Canacini: Dynomiellina)**.** This genus is known only from the Afrotropical and Australasian Regions (Munari & Mathis 2010). Of the seven species in *Isocanace*, five occur in the Afrotropical Region and all are in the *briani* species-group (the two remaining species, *I. albiceps* (Malloch, 1925) and *I. crosbyi* Mathis, 1999, belong to the Australasian *albiceps* species-group). The *briani* species-group is distinguished from congeners by the following combination of characters: frontal vitta with scattered setulae medially; 3 dorsoclinate genal setae; anterior notopleural seta distinctly smaller than posterior seta or lacking; and katepisternal seta present, although sometimes pale. Nothing is known regarding the immature stages, or the biology of these species, except for brief comments on habitats where specimens have been collected. Mathis (1999) provided an identification key to known species of this genus and Munari *et al*. (2021) an identification key to Afrotropical species.

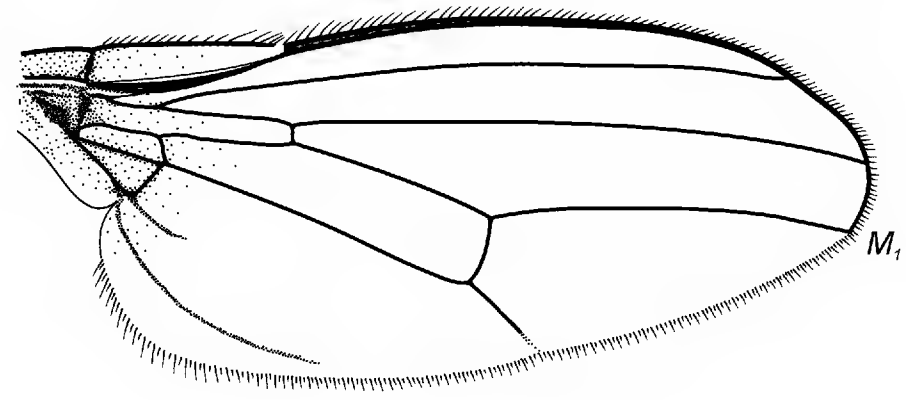
***Nocticanace* Malloch** (Canacinae: Nocticanacini)**.** This is the most species-rich genus of Canacinae (38 species) and demonstrates greater species diversity in the Old World than in the New (Munari & Mathis 2010). The Afrotropics have eight species that occur mainly along the east and southern African coasts, including Madagascar and Seychelles (*N. taprobane* Mathis, 1982, described from Sri Lanka, also occurs in Sierra Leone (Munari 2013)). This genus is mainly distinguished by the following combination of characters: 1–2 interfrontal setae; postocellar setae either much reduced or lacking; 3 lateroclinate, fronto-orbital setae; and katepisternal seta well-developed. The immature stages are unknown. Mathis & Freidberg (1991) provided an identification key to species-groups of *Nocticanace,* including those for Afrotropical species.



15 *Horaismoptera*



16 *Canacea*



17 *Xanthocanace*

Figs 94.15–17. Wings of Canacidae: (15) wing of *Horaismoptera vulpina* Hendel; (16) same, *Canacea macateei* Malloch (non-Afrotropical); (17) same, *Xanthocanace ranula* (Loew) (non-Afrotropical). Fig. 15 (after Munari 1998, fig. 19.7), Fig. 16 (after Mathis 1998, fig. 20.2).

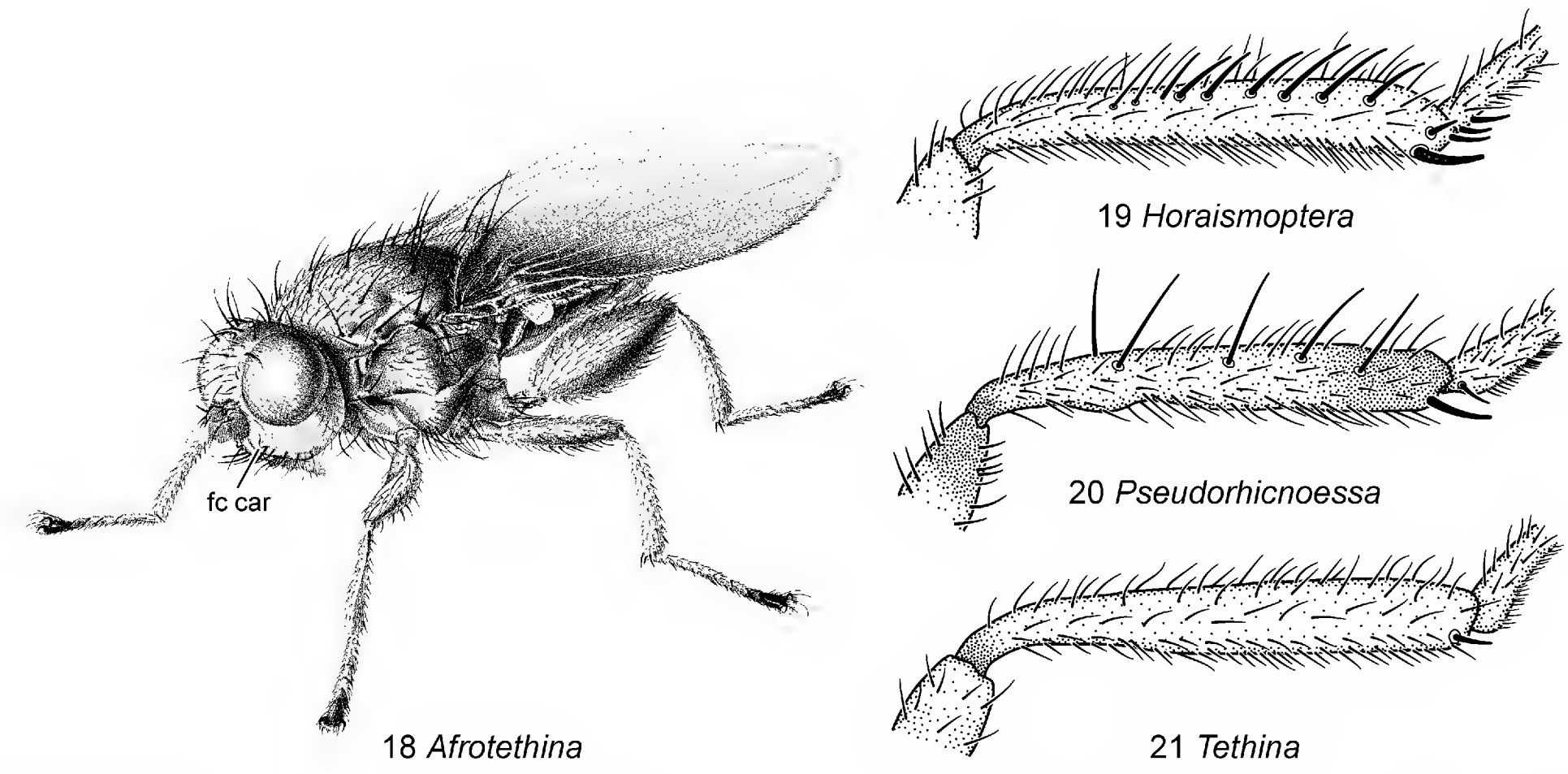
Abbreviations: A_1 – first branch of anal vein; *bm* – basal medial cell; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *dm* – discal medial cell; M_1 – first branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *Sc* – subcostal vein; sp – spine.

***Pelomyiella* Hendel** (Pelomyiinae)**.** With the exception of *Pelomyiella*, which is Holarctic in distribution, the genera of Pelomyiinae are found primarily in the New World. This subfamily is recorded here for the first time from the Afrotropical Region, based on a single female of *Pelomyiella* cf. *mallochi* (Sturtevant, 1923). This unique specimen was collected in Kenya (Lake Naivasha), and represents the first record of the subfamily Pelomyiinae for the Afrotropical Region. The genus *Pelomyiella* includes eight species, five of which are recorded from the Palaearctic Region. The distribution of *Pelomyiella mallochi* ranges from North America, through Europe, to Mongolia.

***Procanace* Hendel** (Canacinae: Nocticanacini)**.** Globally there are 31 species in *Procanace* with all but one, *P. dianneae* Mathis, 1988 (coast of the western Atlantic), occurring in the Old World and the Australasian/Oceanian Region. *Procanace* is especially diverse in the far eastern Palaearctic, Oriental and Oceanian Regions. The Afrotropical species of *Procanace* are assigned to two species-groups: the *fulva* species-group, with two species, and the *grisescens* species-group, with three species (Mathis & Freidberg 1991). Within Canacinae, there is evidence that *Procanace* is the sister-group to all other lineages in the subfamily (Mathis & Foster 2007). This genus is mainly distinguished by the following combination of characters: interfrontal setae absent; 3 lateroclinate fronto-orbital setae; 2 large dorsoclinate genal setae; anteroclinate genal seta moderately well-developed; anterior and posterior notopleural setae present, subequal; and katepisternal seta usually present (lacking in species of the *grisescens* species-group). The immature stages remain unknown. Mathis & Freidberg (1991) provided an identification key to species-groups of *Procanace*, including Afrotropical species.

***Pseudorhicnoessa* Malloch** (Tethininae)**.** An Indo-Pacific genus that only includes three species: *P. longicerca* Munari, 2014, hitherto only known from Papua New Guinea, *P. spinipes* Malloch, 1914, widely occurring throughout the western Pacific and its vicariant species *P. rattii* Munari, 1981, inhabiting the seashores of the Indian Ocean. Although these species are strikingly similar externally, their male terminalia are very different and well-characterised. In the Afrotropical Region *P. rattii* is hitherto known only from Mauritius and Seychelles. Other citations are from the western Oriental Region (India and Sri Lanka). The genus is mainly distinguished by the following combination of characters: a strong, sub-shiny bulge above vibrissal angle present; mid and hind tibiae (Fig. 20) with strong anterodorsal and posterodorsal setae; at least hind femur and tibia bearing an apical dark brown ring; scutellar disc with scattered setulae in addition to major marginal setae; and costal vein of wing abbreviated, only reaching apex of vein R_{4+5}. The immature stages remain unknown. With only one known species in the Afrotropics, the above identification key to genera will distinguish this species.

***Suffomyia* Freidberg** (Zaleinae)**.** An Indo-Pacific genus that only includes four species, two of which, *i.e.*, *S. dancei* Munari, 2008 and *S. scutellaris* Freidberg, 1995, are known exclusively from the Sinai-Arabian area. For the Afrotropical Region, the two species are recorded from Oman. Due to the tiny size of these flies, many other undescribed species are expected to be discovered. The genus is easily distinguished from other

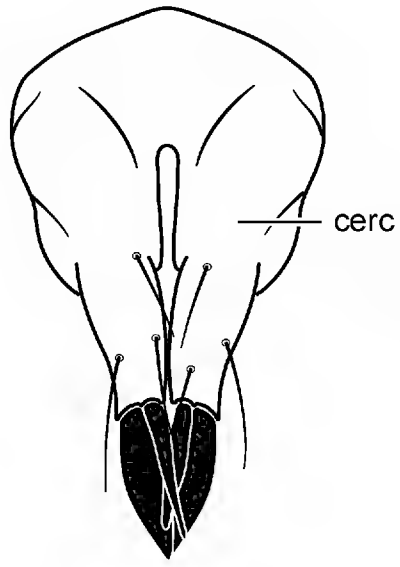


Figs 94.18–21. Habitus and hind tibiae of Canacidae: (18) habitus of *Afrotethina femoralis* (Munari); (19) left hind tibia of *Horaismoptera vulpina* Hendel, anterior view; (20) same, *Pseudorhicnoessa spinipes* Malloch; (21) same, *Tethina grisea* (Fallén). Fig. 18 (after Mathis & Munari 1996, frontispiece), Figs 19–21 (after Munari 1998, figs 19.9–11).

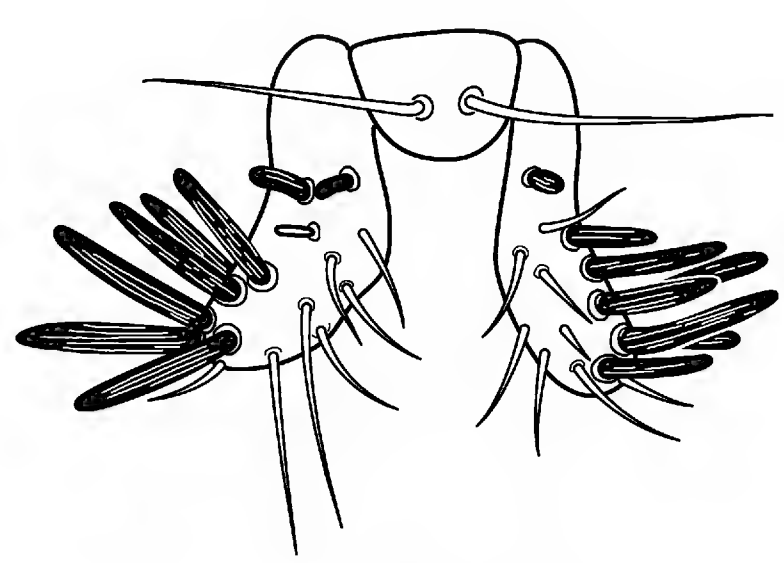
Abbreviation: fc car – facial carina.

canacid flies by the characters provided in the above identification key. McAlpine (2007) provided a very exhaustive treatment of the subfamily Zaleinae, also including an identification key to genera and species, as well as a complete set of diagnostic features for the two genera of this subfamily, *Suffomyia* Freidberg and *Zalea* McAlpine.

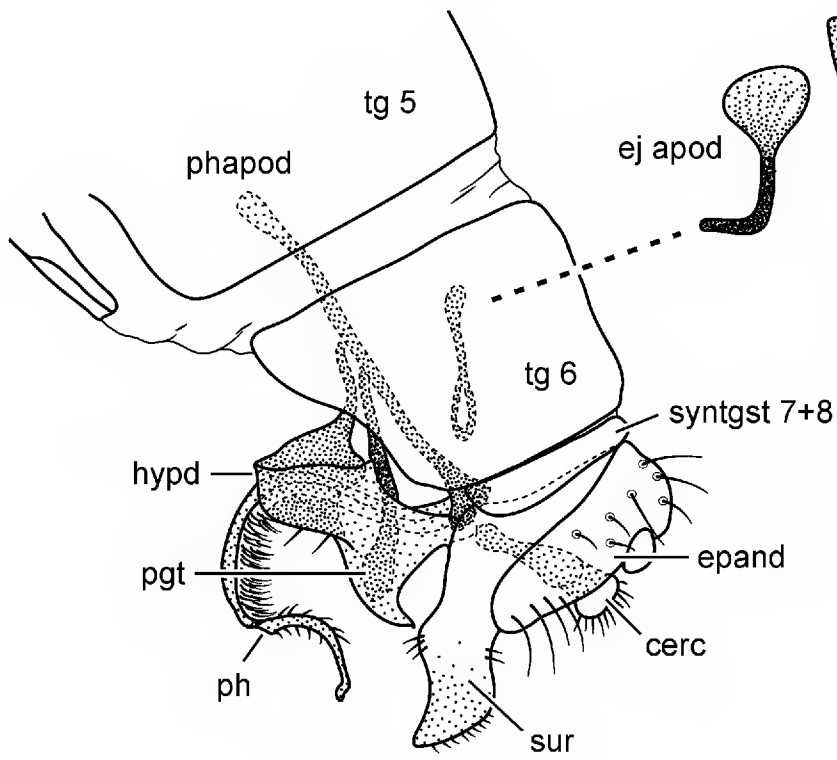
***Tethina* Haliday *in* Curtis** (Tethininae)**.** Among genera of Canacidae, *Tethina* is by far the most species-rich globally, with two-thirds (78 species) of the 117 described species currently recognised in the subfamily Tethininae (Munari & Mathis 2010). Sixteen species of *Tethina* are known from the Afrotropical Region (half of them exclusively from Oman or the United Arab Emirates) and occur on coasts of both the Atlantic and Indian Oceans. *Tethina* is distinguished from other genera of the subfamily Tethininae by the following combination of characters: frons bearing some setulae in addition to larger setae; 3–4 lateroclinate fronto-orbital setae, sometimes slightly reclinate; postocellar setae convergent (absent only in the west Palaearctic species *T. lusitanica*); a distinctive shiny tubercle present near, or above, the vibrissal socket; eye bare; gena bare, except for a ventral, or nearly ventral, row of slightly upwardly oriented setae (subvibrissal setae); scutum with more or less numerous rows of setulae; scutellar disc bare; postpronotum usually with 3 setae; acrostichal setulae in 2, or more, complete, or nearly complete, rows; prescutellar acrostichal



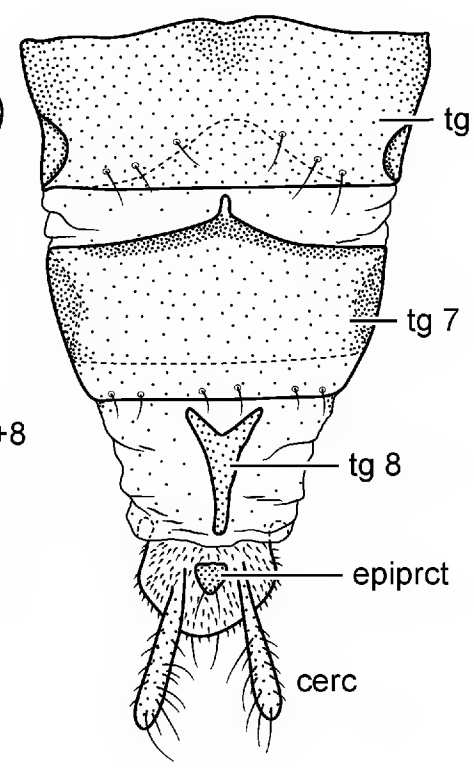
22 *Canace* ♀



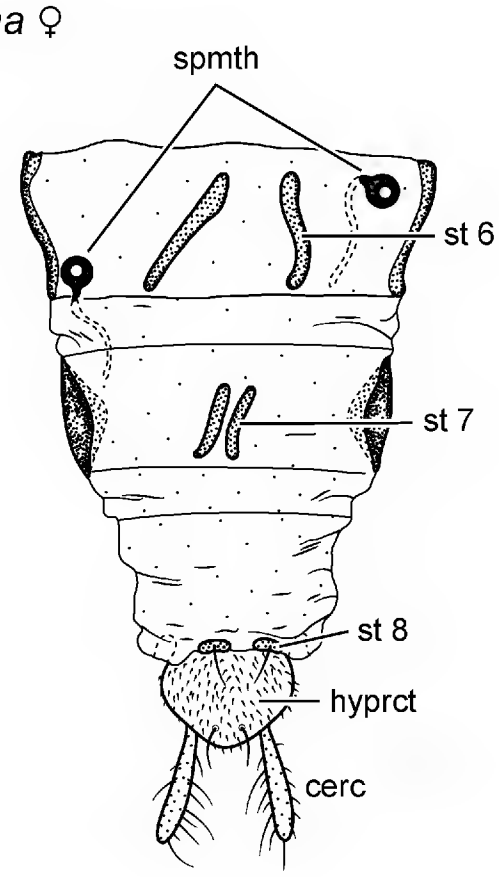
23 *Tethina* ♀



24 *Tethina* ♂



25 *Tethina* ♀



26 *Tethina* ♀

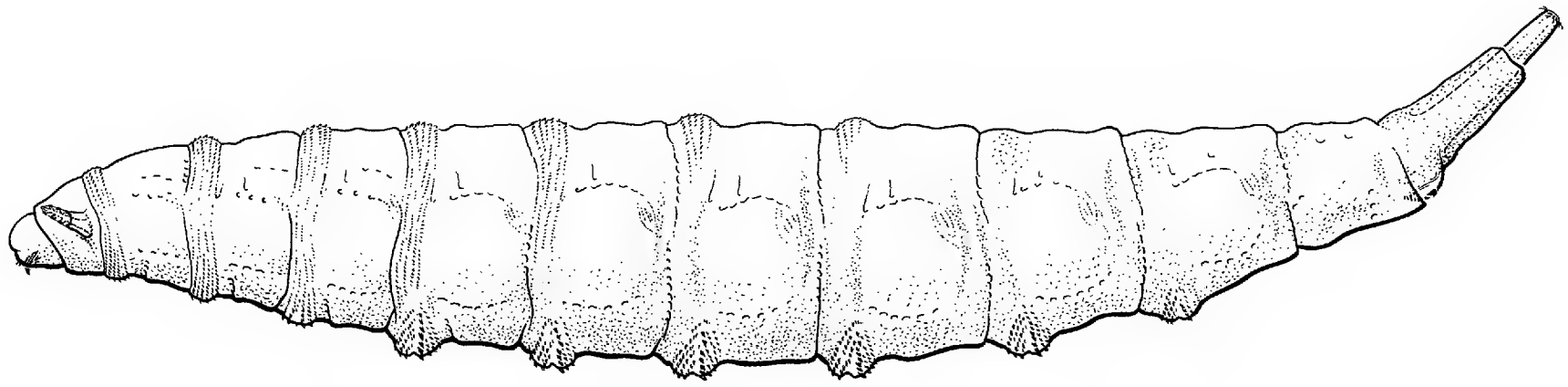
Figs 94.22–26. Male and female terminalia of Canacidae: (22) female cerci of *Canace nasica* (Haliday); (23) same, *Tethina albo-guttata* (Strobl); (24) male postabdomen of *T. albosetulosa* (Strobl), lateral view; (25) female postabdomen of *T. albosetulosa* (Strobl), dorsal view; (26) same, ventral view. Fig. 22 (after Mathis 1982*b*, fig. 12), Fig. 23 (after Freidberg & Beschovski 1996, fig. 30), Figs 24–26 (after Munari 1998, figs 19.12–14).

Abbreviations: cerc – cercus; ej apod – ejaculatory apodeme; epand – epandrium; epiprct – epiproct; hypd – hypandrium; hyprct – hypoproct; pgt – postgonite; ph – phallus; phapod – phallapodeme; spmth – spermathecae; st – sternite; sur – sursty-lus; syntgst – syntergosternite; tg – tergite.

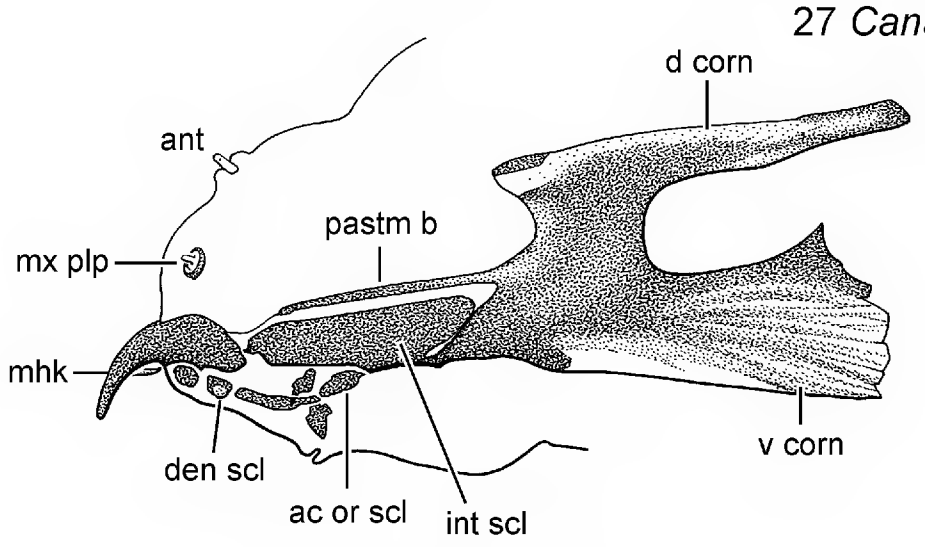
setae usually present; costal vein not spinose; vein *CuA+CuP* short, usually shorter than basal medial cell (*bm*); discal medial cell (*dm*) distinct; anterior surstylus lacking; posterior surstylus usually broadly articulated laterally with ventral margin of epandrium (Fig. 24); and phallus ribbon-like, very long and sinuous. The immature stages are very poorly known. There is no identification key to Afrotropical species.

***Trichocanace* Wirth** (Canacinae: Canacini: Dynomiellina)**.** A genus of three described species that occurs primarily in the Australasian/Oceanian and Oriental Regions (Munari & Mathis 2010), with only one species, *T. sinensis* Wirth, 1951, also occurring in East Africa (Kenya and Madagascar). *Trichocanace* is distinguished from other genera of Canacinae by the following combination of characters: frons uniformly micro-tomentose; anteroclinate genal seta small and pale; 2 dorsoclinate genal setae present; arista with apical ⅓–½ bare; anterior notopleural seta absent; postpronotum bearing setulae and prominent seta; katepisternal seta absent; and only one pair of lateral scutellar setae present. The immature stages remain unknown. Mathis (1982*a*) provided an identification key to Afrotropical species.

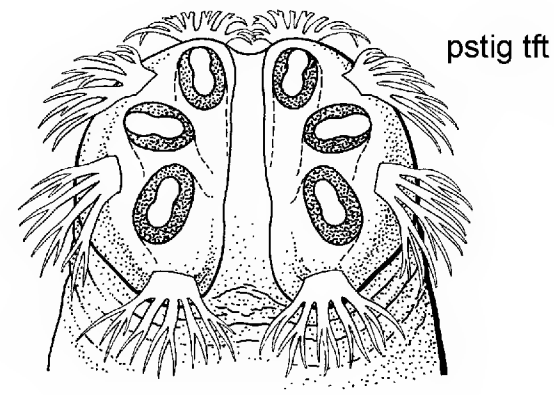
***Xanthocanace* Hendel** (Canacinae: Canacini: Dynomiellina)**.** A genus of 12 described species occurring in the Afrotropical Region and Indo-Pacific area. Five species occur in the



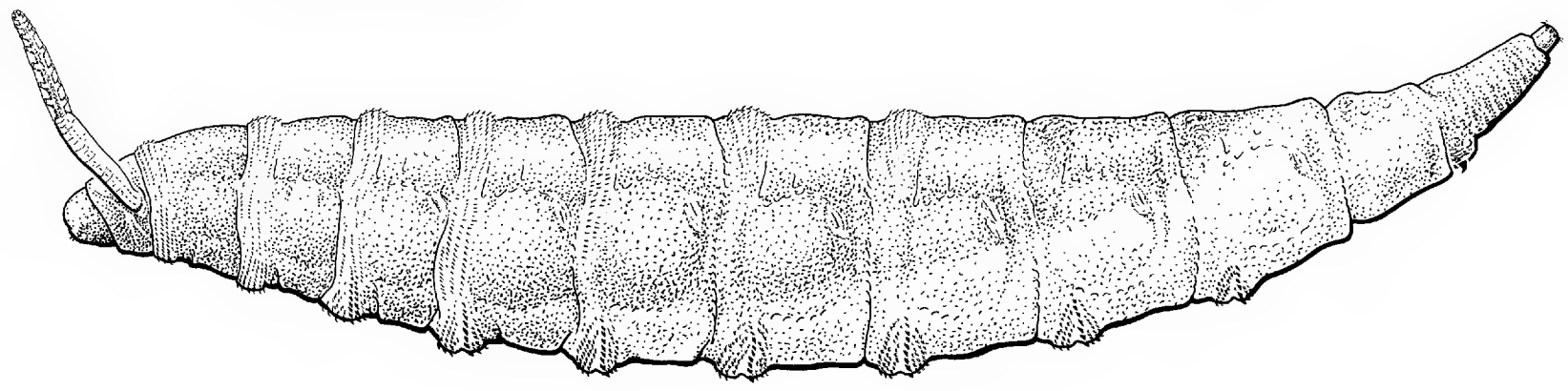
27 *Canacea*



28 *Canacea*



29 *Canacea*



30 *Canacea*

Figs 94.27–30. Immature stages of Canacidae: (27) third-instar larva of *Canacea macateei* Malloch (non-Afrotropical), lateral view; (28) same, anterior end, lateral view (indicating cephaloskeleton); (29) same, posterior spiracle, caudal view; (30) same, puparium, lateral view. Figs 27–30 (Wirth 1987, figs 7–10).

Abbreviations: ac or scl – accessory oral sclerite; ant – antenna; d corn – dorsal cornu; den scl – dental sclerite; int scl – intermediate sclerite; mhk – mouthhook; mx plp – maxillary palpus; pastm b – parastomal bar; pstig tft – peristigmatic tuft; v corn – ventral cornu.

Afrotropics, namely: *X. capensis* Wirth, 1956 (Cape Province, South Africa), *X. hamifer* Munari, 2008 (United Arab Emirates), *X. kaplanorum* Mathis & Freidberg, 1982 (Oman and United Arab Emirates), *X. sabroskyi* Mathis & Freidberg, 1982 (Oman and United Arab Emirates) and *X. zeylanica* Delfinado, 1975 (Oman). Of the seven genera comprising the tribe Canacini, *Xanthocanace* is the most species-rich genus. *Xanthocanace* is distinctive among genera of Canacinae by the following combination of characters: setae generally pale; frons uniformly and densely micro-setulose; 4–6 lateroclinate, fronto-orbital setae present; antennal arista with apical ⅓–½ bare, style-like; anteroclinate genal seta small and pale; 2 dorsoclinate genal setae present; anterior notopleural seta well-developed; 2 pairs of lateral scutellar setae present; katepisternal seta absent; and wing vein M_1 with last section arcuate or very slightly so. The immature stages remain unknown. Mathis (1982*a*) provided an identification key to species, although only eight species (including *X. capensis*) were then known.

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MILICHIIDAE 95

(Milichiid Flies, Free-loader Flies or Ant-mugging Flies)

John E. Swann and Bradley J. Sinclair

Fig. 95.1. Male of *Milichiella* sp. (Tanzania) (photograph © S.A. Marshall).

Diagnosis

Small-sized (body length: 1–7 mm) acalyptrate flies, often largely brown or black, occasionally orange or yellow in colour, often dull to shiny (Fig. 1); males of some genera with silvery pruinosity on abdomen.

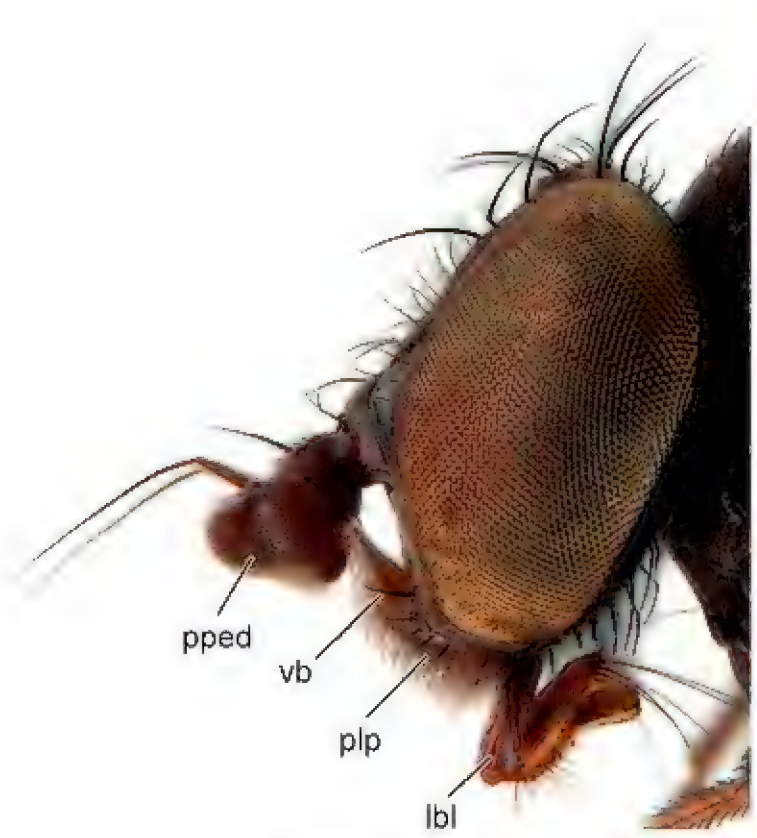
Head generally higher than long (Figs 2–5, 31, 33); eyes bare; gena linear to broad; inner and outer vertical setae present; postocellar setae parallel (Figs 19–21, 24, 26–28, 31, 33), subparallel, or cruciate at tips (Figs 19–21); frons usually with 2 or 3 pairs of inclinate frontal setae, 2 or 3 pairs of latero-clinate to proclinate orbital setae (Figs 3–5, 17–21); rarely with row of 4–10 pairs of reclinate fronto-orbital setae (males of *Enigmilichia* Deeming and *Milichia distinctipennis* Deeming species-group) (Fig. 8); frons broader than width of eye in both sexes, but in Milichiinae sometimes narrower in male than female, usually with rows of interfrontal setae or setulae, sometimes confined to 2 distinct fasciae or sclerotised interfrontal strips (Fig. 23); lunule usually well-developed, often with 1 or 2 pairs of setulae (Fig. 20); lower margin of face sometimes warped upwards (Fig. 26); vibrissa strong, lying near lower eye margin (Figs 20, 21) or shifted above eye margin; lower margin of gena with subvibrissal setae (Fig. 22); antenna usually short and decumbent, with postpedicel oval and enlarged in some males (Figs 2–5); arista usually slender, micro-pubescent, densely long setose in *Aldrichiomyza* Hendel (Fig. 17); proboscis often conspicuously elongate, geniculate (Figs 17, 33); palpus short to elongate, greatly enlarged in some males; 2 or 4 pseudotracheae present.

Thorax with scutum convex, polished and shiny to thickly setose; prosternum small, isolated or fused laterally forming precoxal bridge; 1–2 postpronotal setae; proepisternal seta present; 2 pairs of scutellar setae, without discal setulae; proepimeral seta usually absent; anepisternum with setulae and strong setae in some species (Figs 5, 7, 29); katepisternum with 1–3 setae (Figs 3, 21, 22, 29). Wing with humeral and

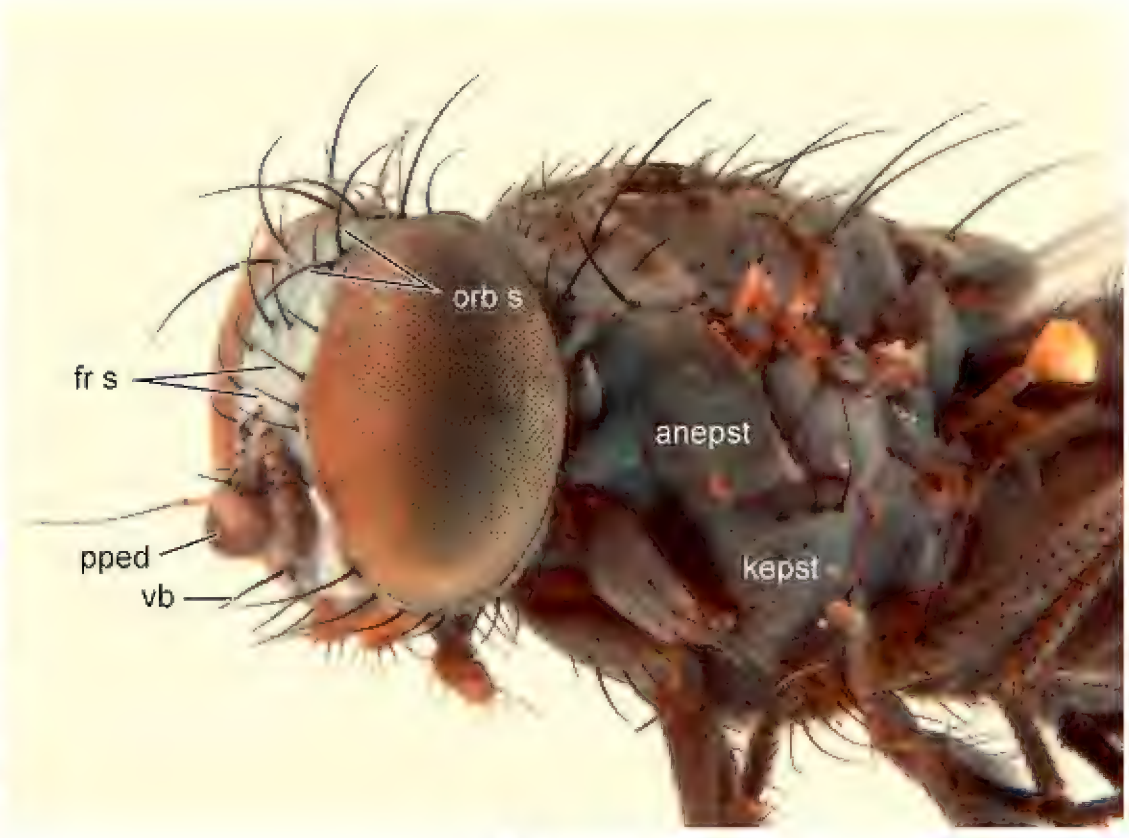
Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2021. Manual of Afrotropical Diptera. Volume 3. Brachycera—Cyclorrhapha, excluding Calyptratae. *Suricata* 8. South African National Biodiversity Institute, Pretoria; pp. 2015–2034.

subcostal breaks (Fig. 9), region of latter often modified into costal lappet (Fig. 10); costal vein (*C*) extended to veins M_1 or to R_{4+5} in *Aldrichiomyza*, *Paramyia* Williston (Figs 12, 13) and *Xenophyllomyza* Ozerov (non-Afrotropical); subcostal vein (*Sc*) usually complete, often pale and inconspicuous distally (Fig. 9); crossvein *dm–m* usually present (Figs 9–12, 14–16); veins R_{4+5} and M_1 converging in some genera (Figs 9–11); cell *cua* closed, small (Fig. 9); vein *CuA+CuP* short, not reaching wing margin (Fig. 10); anal lobe usually well-developed (Fig. 9). Legs usually without features; tibiae without preapical dorsal setae; hind tibia often expanded in male *Leptometopa* Becker (Fig. 27); narrow tibial organ usually present in depression on hind tibia of both sexes of *Madiza* Fallén.

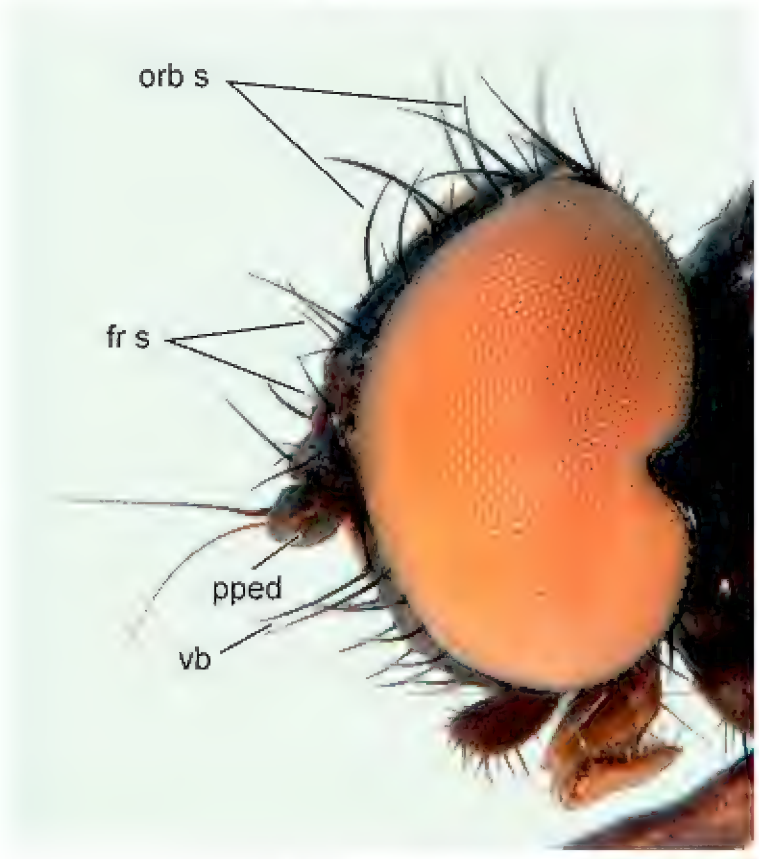
Abdomen slender to broadened and flattened (especially in males of species with tergites conspicuously clothed in silvery



2 *Milichia*



3 *Milichia*



4 *Milichiella*

5 *Pholeomyia*

Figs 95.2–5. Heads and heads and thoraces of Milichiidae: (2) head of *Milichia patrizii* Hennig, lateral view ♂; (3) head and thorax of *Milichia* sp., lateral oblique view ♂; (4) head of *Milichiella* sp., lateral view ♂; (5) head and thorax of *Pholeomyia* sp., lateral view ♀ (non-Afrotropical).

Abbreviations: anepst – anepisternum; fr s – frontal setae; kepst – katepisternum; lbl – labellum; orb s – orbital setae; plp – palpus; pped – postpedicel; vb – vibrissa.

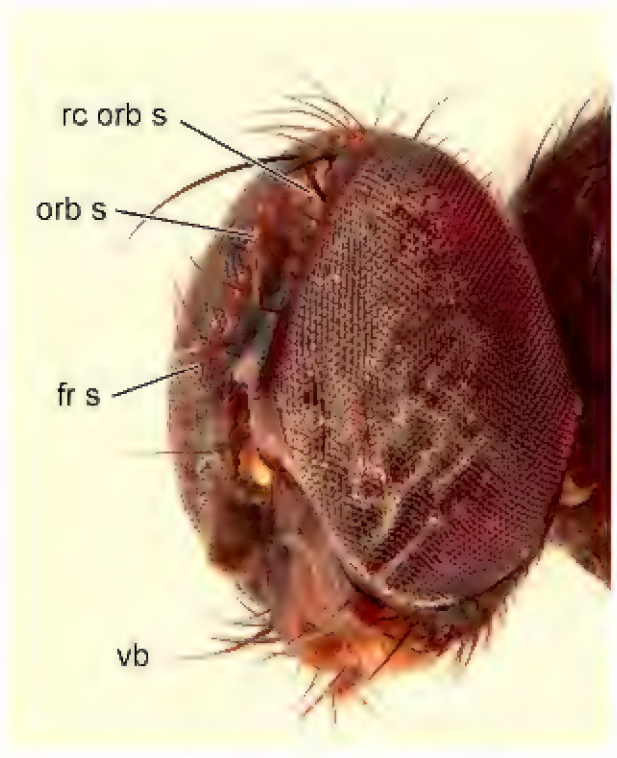
pruinescence); sternite 5 generally similar to sternite 4, strongly reduced in some genera (Fig. 35); seven pairs of spiracles present; male and female terminalia and male pregenital segments studied in detail by Brake (2000); pregenital sclerites generally asymmetric (Fig. 35), including tergite 6 in some genera, syntergosternite 7 + 8 with spiracular pairs 6 and 7; epandrium mostly saddle-shaped (Figs 35, 36); surstylus usually articulated (Figs 35, 36); hypandrium often ring-shaped, with bacilliform sclerite articulated with hypandrium and extended to inner side of surstylus (Figs 35, 36); pregonites fused with hypandrium, postgonites absent; phallapodeme free or fused with hypandrium; phallus with short and glabrous distiphallus, secondarily lengthened and more membranous; cercus small to large, setose, membranous or ventral margin sclerotised (Figs 35, 36); female segments 6–8 or 7–8 retracted, with sclerites undivided or divided (Figs 37, 38); 2 spermathecae present, with extremely elongate coiled ducts and non-sclerotised receptacles (Fig. 39).

Adult Milichiidae are generally recognisable based on the arrangement of head setation, humeral and subcostal breaks and closure of the anterior cubital wing cell (*cua*). Some Carnidae (see Chapter 93), with similar head setation, have a bulbous prementum, lack the closed cell *cua*, lack lunular setae and all Carnidae have postgonites in males. Chloropidae (see Chapter 96) have a similar general appearance, but lack the humeral break and cell *cua* and generally have more rudimentary head setation than milichiids.

Biology and immature stages

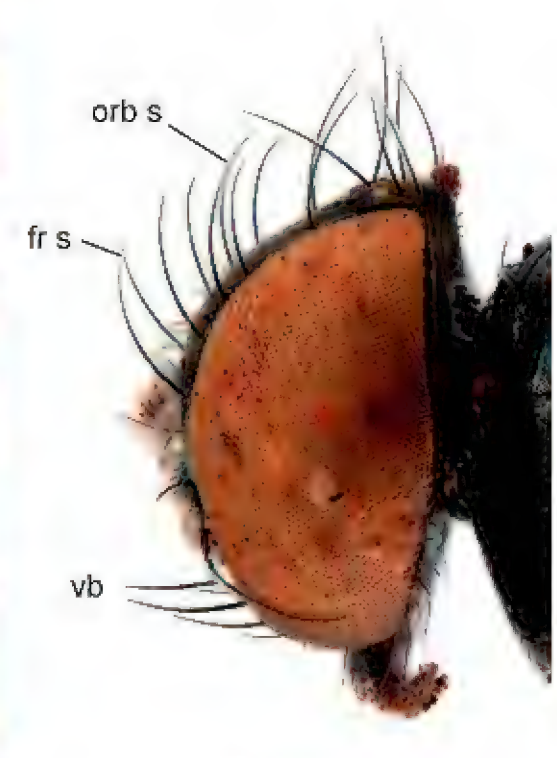
The biology of most Milichiidae species remains unknown, but known milichiid larvae appear to be general saprophages or coprophages (Brake 2000; Papp & Wheeler 1998: 321; Sabrosky 1977: 270, 1987*a*: 904; Swann 2000: 265, 2010: 1125). Ferrar (1987: 222) provided a thorough overview of larval habits, noting that these develop in decaying matter, ranging from rotting fish and animal dung to decomposing plant material. He further noted that the widespread and species-rich genus *Desmometopa* Loew has numerous species reared from decaying fruits and vegetation. Most recently, Brake (2011) noted specimens of the Afrotropical species *D. leptometopoides* Sabrosky, 1983, reared from the fruit of Bitter melon, *Momordica charantia* L. (Cucurbitaceae). Kumara *et al.* (2010) noted puparia of *Desmometopa* species associated with a human cadaver in Malaysia and milichiids are commonly found in association with human forensic studies (Avila & Goff 1998; Gunatilake & Goff 1989; Shalaby *et al.* 2000).

In addition to these more mundane lifestyles, larvae of numerous milichiids have a close association with Hymenoptera. Melo (1996), for example, recorded a species of an undescribed milichiid genus breeding as inquilines in the nests of a species of stingless bee, *Melipona* Illiger (Apidae) in Brazil. In the Nearctic Region, Krombein (1967: 413) recorded larvae of the non-Afrotropical genus *Eusiphona* Coquillett, feeding on pollen in a Megachilidae bee nest. None of the six species of milichiids (in four genera), that are known to have larvae associated with ants' nests occur in the Afrotropics (Ferrar 1987: 224). The larvae of *Milichia argyratoides* Collin, 1922, have been noted on tree wounds in Nigeria, with *Crematogaster* Lund (Formicidae) ants tending them. Larvae were covered with excreta, which ants fed upon and wandered through the ant runs, but were not found in the ants' nests (Farquharson 1922). Some species of *Phyllomyza* Fallén occur in association with Formicinae and Ponerinae ants in the Palaearctic and Oriental Regions (Ferrar 1987: 225; J.E. Swann, pers. obs.) and these groups of ants may also be hosts of *Phyllomyza* species in the Afrotropics. Several Neotropical milichiid genera are only known from arboreal ants' nests and it may be worth



6 Undescribed genus A

7 Undescribed genus A



8 *Milichia*

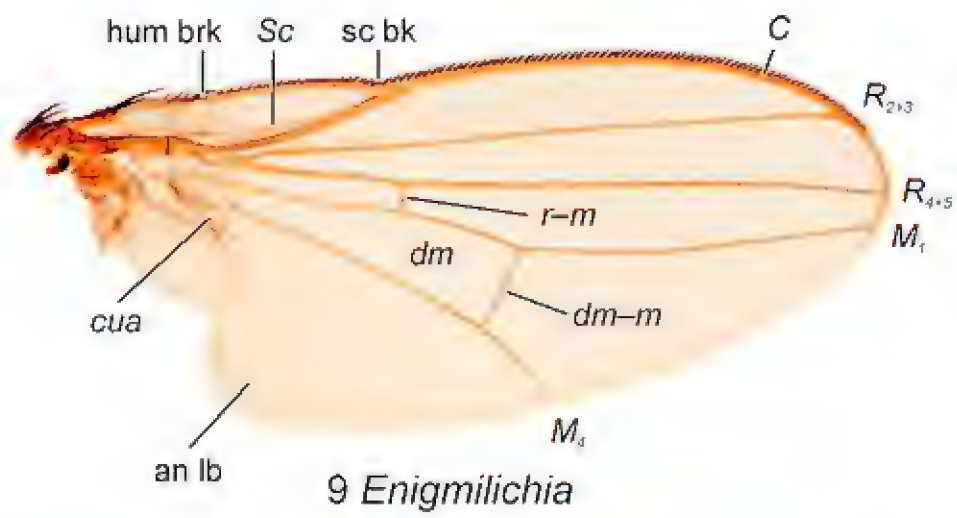
Figs 95.6–8. Heads and thorax of Milichiidae: (6) head of Undescribed genus A, lateral oblique view ♂; (7) same, thorax, lateral view; (8) head of *Milichia distinctipennis*-group, lateral view ♂.

Abbreviations: anepst – anepisternum; fr s – frontal seta; orb s – orbital seta; rc orb s – reclinate orbital seta; vb – vibrissa.

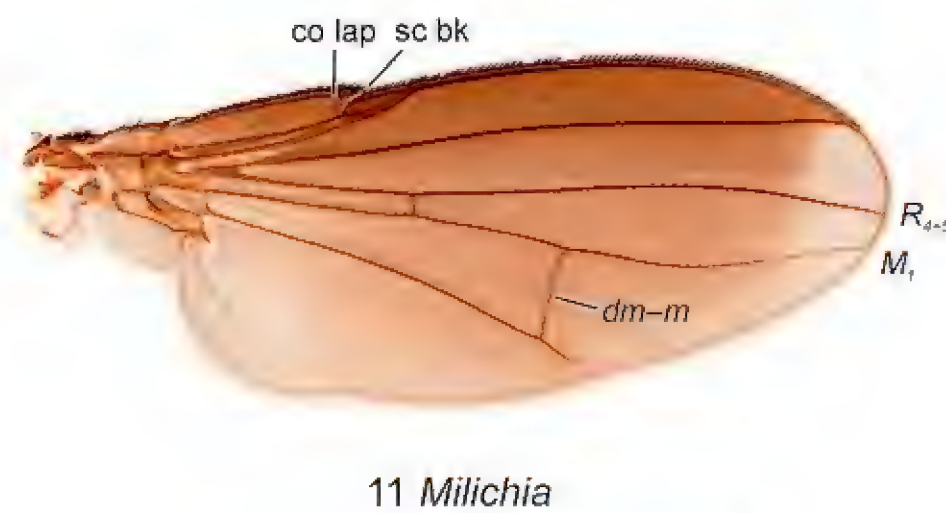
investigating Afrotropical arboreal ant nests for rare and undescribed Afrotropical milichiids.

The propensity for milichiids to be found as inquilines in ants' nests and as kleptoparasites has led to numerous vernacular names being applied to the group, such as "freeloader flies", "jackal flies" and "ant-mugging flies". Such names have been used to simplistically illustrate what are in actuality very complex evolutionary interactions. Wild & Brake (2009) detailed the complex interactions between adults of some species of *Milichia* Meigen and various species of Myrmicinae ants. In the cases of Afrotropical species, *M. dectes* Collin, 1922, *M. proectes* Collin, 1922 and *M. prosaetes* Collin, 1922, have all been recorded soliciting food regurgitated by *Crematogaster* ants; more specifically *C. buchneri* Forel, in the case of *M. dectes*. Two South-east Asian *Milichia* species have also been recorded "licking" the anal secretions of species of *Creamtogaster* and *Dolichoderus* Lund ants (Wild & Brake 2009). *Milichia farquharsoni* Collin, 1922 and *M. patrizii* Hennig, 1952 are thought to have modified antennal pedicels and the clypeal membrane between the palpi and proboscis (Fig. 2) aids in kleptoparasitic feeding, by controlling the ants' movements and forcing regurgitation of food from ants (Wild & Brake 2009). Deeming (1998: 147) and Farquharson (1919, 1922) noted this association of *Milichia* adults and ants and such associations may be widespread for most species of the genus. Besides *M. argyratoides* on tree wounds being tended by ant larvae, other *Milichia* species have larvae that have been reared from various types of dung and from dead fish (Bohart & Gressitt 1951; Ferrar 1987: 223).

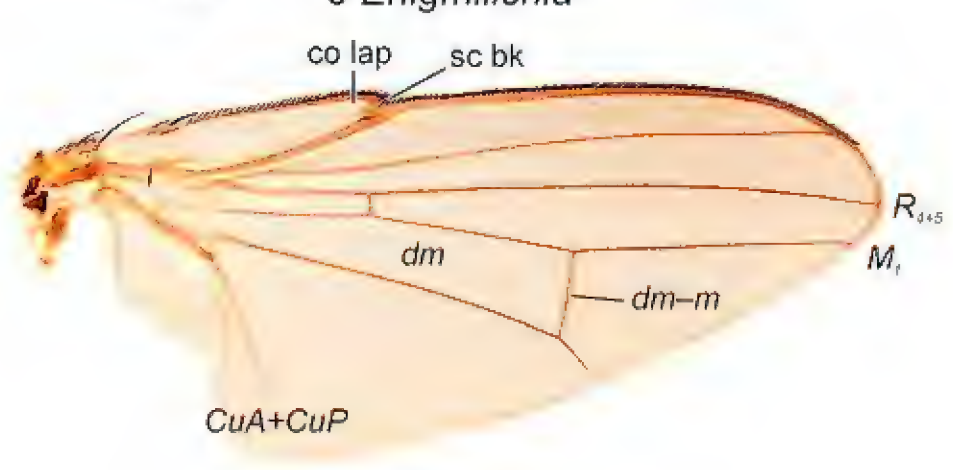
Two Nearctic species of *Pholeomyia* Bilimek have been recorded from refuse heaps in nests of the ant *Atta texana* (Buckley) (Formicidae) (Waller 1980), while adults of the Neotropical species *Pho. dampfi* Sabrosky, 1959, have been recorded pursuing bats deep into caves in Guatemala, where their larvae develop in bat guano (Sabrosky 1959). Papp (1978) further recorded an adult of *Pho. leucozona* Bilimek, 1867, from a cave in Guatemala and it is reasonable to assume the species is also associated with bat guano in the larval stages. Given that *Pho. politifacies* Sabrosky, 1959 is the only described species in the genus known from the Afrotropics, and also occurs in the Neotropics, it is likely to be guanobious, given that the ant genus *Atta* L. is restricted to the New World. Development in bat guano has also been documented by Ferreira & Martins (1999) for the genus *Milichiella* Giglio-Tos and other genera, including *Leptometopa* and *Phyllomyza*, have been recorded as adults from caves (Papp 1978, 1982, 1984; Sabrosky 1964). Kirk-Spriggs (1987) recorded large numbers of the Oriental species, *Phy. cavernae* de Meijere, 1914, associated with bat caves in northern Sulawesi, Indonesia. Undescribed species of *Leptometopa*, *Milichia* and *Phyllomyza* are known, sampled from bat guano in Afrotropical caves and it is reasonable to assume larvae to be guanobious in such cases.



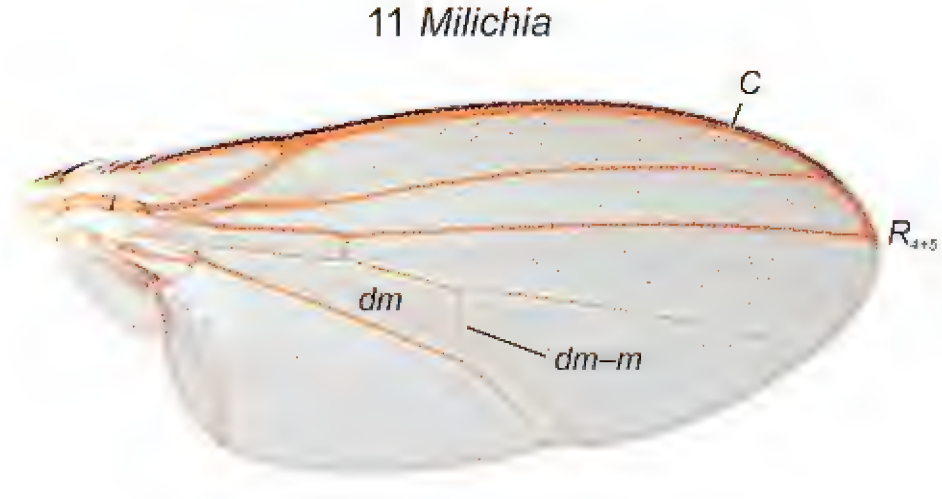
9 *Enigmilichia*



11 *Milichia*



10 *Milichia*



12 *Aldrichiomyza*

Figs 95.9–12. Wings of Milichiidae (dorsal views): (9) *Enigmilichia* sp. ♂; (10) *Milichia* sp. ♂; (11) *Milichia distinctipennis* Deeming ♀; (12) *Aldrichiomyza* sp. ♀ (non-Afrotropical).

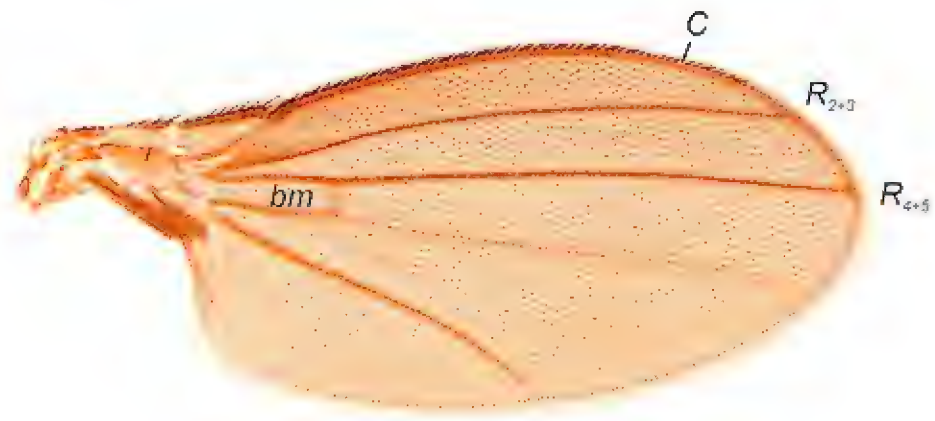
Abbreviations: an lb – anal lobe; *C* – costal vein; co lap – costal lappet; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *dm* – discal medial cell; *dm–m* – discal medial crossvein; hum brk – humeral break; M_1 – first branch of media; M_4 – fourth branch of media; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Sc* – subcostal vein; sc bk – subcostal break.

Many adult milichiid flies have fascinating kleptoparasitic biologies. Sivinski *et al*. (1999) list the genera *Desmometopa*, *Leptometopa* (as *Desmometopa latipes*), *Milichiella*, *Neophyllomyza* Melander, *Paramyia* and *Phyllomyza*, as having species with adults that are kleptoparasitic on a wide range of predaceous arthropods. Large orb-weaving spiders of the genus *Nephila* Leach (Araneidae) have been observed with species of *Desmometopa*, *Milichiella*, *Neophyllomyza*, *Paramyia* and *Phyllomyza* feeding on partially digested prey items (Eisner *et al*. 1991; Robinson & Robinson 1977; Sivinski & Stowe 1980). Robinson & Robinson (1977) hypothesised from their observations that species of *Phyllomyza* may be associated with the same spider for a prolonged period of time, only leaving their perch on the cephalothorax to feed. Given that all observed *Phyllomyza* were females and that the spider egg parasitoid *Conioscinella* Duda (Chloropidae) exhibits the same type of adult feeding behaviour with *Argiope* Audouin (Araneidae) spiders, it is feasible that some *Phyllomyza* may also be egg parasitoids of *Nephila* spiders.

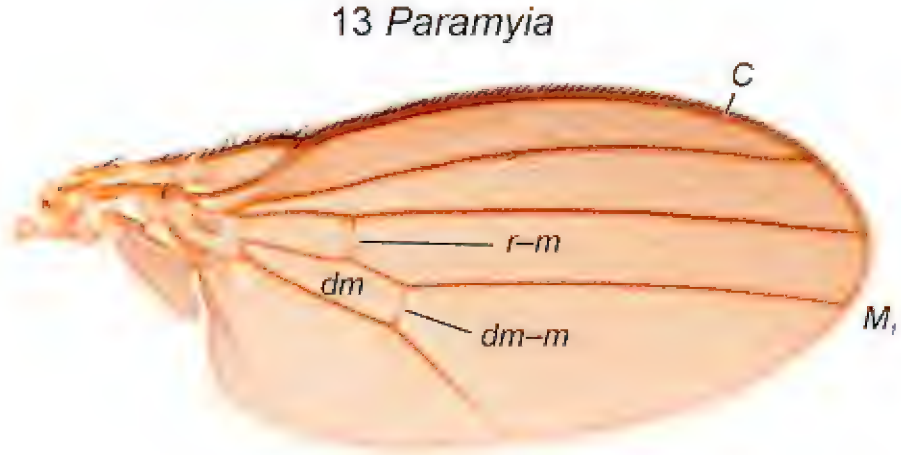
Robinson & Robinson (1977) also recorded species of *Neophyllomyza* feeding on a stingless bee being digested by a reduviid bug in Panama. Sivinski *et al*. (1999) noted that *Neophyllomyza wulpi* (Hendel, 1907) exhibited a phoretic relationship with New Guinean Asilidae, presumably also as kleptoparasites. Eisner *et al*. (1991) noted that species of *Desmometopa*, *Milichiella*, *Neophyllomyza* and *Paramyia nitens* (Loew, 1869), could be attracted to defensive compounds from Coreidae and Pentatomidae (Hemiptera), that were commonly captured in *Nephila* spider webs. Although *Leptometopa latipes* (Meigen, 1830) is documented as a spider kleptoparasite (Sivinski *et al*. 1999), the larvae are also commonly associated with birds' nests (Ferrar 1987: 225). Marshall (2019) described and photographed the phoretic and kleptoparasitic behaviour of an undescribed species of *Paramyia* on a South-east Asian tiger beetle (Coleoptera: Carabidae: Cicindelinae).

Eisner *et al*. (1991) and Sivinski & Stowe (1980) reported that the vast majority of specimens of all milichiid genera collected in association with spiders are female. The extra protein from kleptoparasitic meals may be necessary for egg maturation (Brake 2000) and, as suggested by Robinson & Robinson (1977), associated flies may possibly be egg parasitoids of spiders. Brake (2000) asserted that in addition to nectar-feeding, kleptoparasitic feeding behaviour of females is part of the ancestral behaviour of Milichiidae.

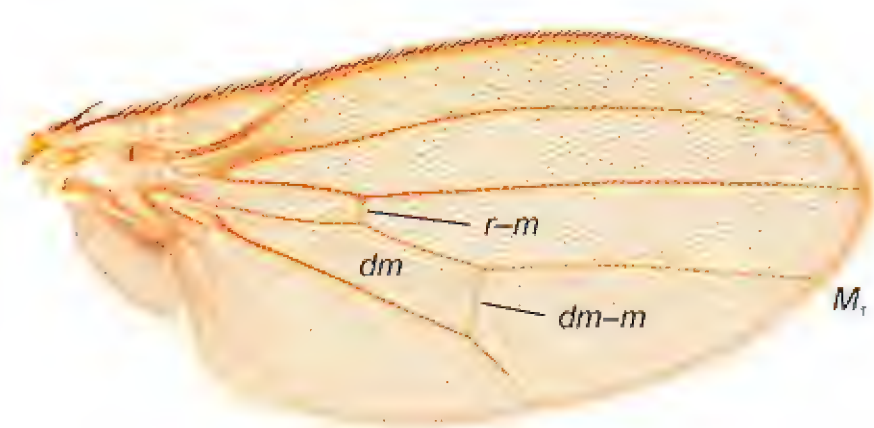
Numerous species in several genera can be sampled at flowers (Brantjes 1980; Heiduk *et al*. 2010; Masinde 2004; Ollerton *et al*. 2009; Papp & Wheeler 1998: 321; Sabrosky 1987*a*: 904, *b*; Wolda & Sabrosky 1986). As with the kleptoparasitic records, the flies sampled as pollinators were all female. Wolda & Sabrosky (1986) noted that there was no oviposition occurring in association with plants and that it was possible that flies were receiving nutrition essential for egg maturation, as is hypothesised for kleptoparasitism. The most thoroughly studied



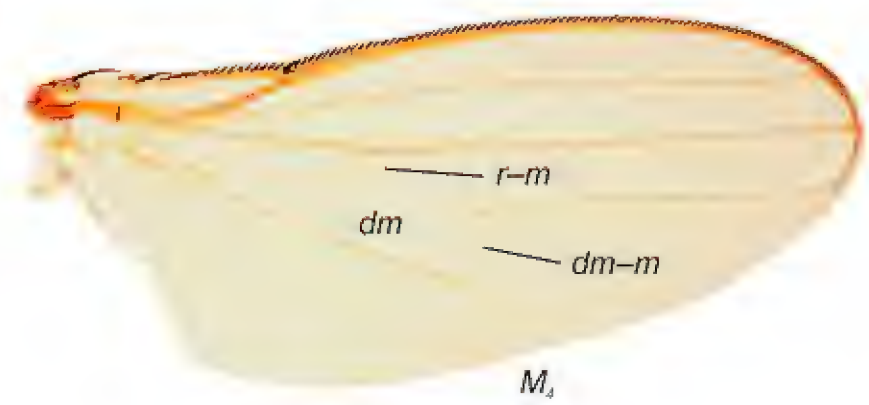
13 *Paramyia*



14 *Neophyllomyza*



15 *Phyllomyza*



16 *Madiza*

Figs 95.13–16. Wings of Milichiidae (dorsal views): (13) *Paramyia* sp. ♀; (14) *Neophyllomyza* sp. ♀; (15) *Phyllomyza* sp. ♀; (16) *Madiza* sp. ♀ (non-Afrotropical).

Abbreviations: *bm* – basal medial cell; *C* – costal vein; *dm* – discal medial cell; *dm–m* – discal medial crossvein; M_1 – first branch of media; M_4 – fourth branch of media; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein.

group with milichiids as pollinators in the Afrotropics is the trap flower genus *Ceropegia* (Asclepiadoideae). Heiduk *et al*. (2010) hypothesised that the genera of milichiids that are attracted to the scent of the flowers are all kleptoparasitic and that the floral scent mimics the odours which attract the flies to prey items. Masinde (2004) found that there was an optimal size of 1.0–2.5 mm to enter flowers and transfer pollinaria onto their proboscis, while looking for the potential feeding site of the flower's nectaries. Sabrosky (1987*b*) described the species *Leptometopa nilssoni* from *Ceropegia albisepta* Jumelle & H. Perrier in Madagascar. Ollerton *et al*. (2009) noted that the genera *Desmometopa*, *Leptometopa*, *Milichiella*, *Neophyllomyza*, *Phyllomyza* and *Stomosis* Melander are all attracted to flowers of *Ceropegia*, but only *Desmometopa*, *Leptometopa* and *Stomosis* were actually pollinators by transferring pollinaria.

In contrast to the females' kleptoparasitic and pollinator behaviours, adult male milichiids have equally well-documented, interesting lekking behaviours. Males of some species of *Milichia sensu lato*, *Milichiella* and *Pholeomyia* have silvery abdomens and form mating swarms that can be seen from long distances (Deeming 1998: 147; Monteith 1982; Sabrosky 1973: 270).

There is an even greater paucity of information on the physical descriptions of the immature stages of milichiids. Sturtevant (1926) noted four long slender filaments on the anterior of the egg of *D. m-nigrum* (Zetterstedt, 1848), which is a virtually cosmopolitan species (including the Afrotropics). The only other two species with described eggs, *Madiza glabra* Fallén, 1820 and *Milichiella tiefii* (Mik, 1887) are both Palaearctic species and lack anterior filaments. Their general appearance can be summarised from Papp & Wheeler (1998: 318) and Roháček (1995). Eggs are white, medium-sized (0.55–0.60 mm in length, 0.13–0.17 mm in width), of a depressed dolioform to depressed ovoid/obovoid (*sensu* Clopton 2004) shape (Fig. 40). There are two slender band-like ridges from the micropyle to at most the anterior third of the egg. The chorion has a complex pattern of micro-sculpture in the form of hexagonal pits. Roháček (1995) based his description of *M. tiefii* (as *M. argyrogaster*) eggs on those dissected from the abdomen of a gravid female. Dissected eggs from gravid females are known for the genera *Leptometopa*, *Neophyllomyza*, *Paramyia*, *Pholeomyia*, *Phyllomyza* and *Stomosis* and all match this general description.

The third-instar larval characters of Milichiidae were reviewed by Ferrar (1987: 226), Papp & Wheeler (1998: 318) and Roháček (1995) and can be summarised from these sources. The larva is slightly to strongly S-shaped (Fig. 41) and measures 4.0–7.2 mm in length, 0.4–0.8 mm in width. Abdominal segments 1–7 have distinct transverse creeping welts, each with anterior and posterior double rows of spinules, on the posterior border of each segment (Fig. 41). The cephaloskeleton (Figs 42–44) is typical of saprophagous Diptera, with curved heavily sclerotised mouthhooks, dental sclerites, long parastomal bars and ventral cibarial ridges present. The mouthhooks articulate with the intermediate sclerite in the genera *Enigmilichia*, *Leptometopa*, *Milichia* (Deeming & Báez 1985) and *Milichiella* (Fig. 43) and in *Desmometopa* and *Pholeomyia* there is an intercalary sclerite between the mouthhooks and the intermediate sclerite (Fig. 44). The prothoracic spiracles have 5–13 spherical or digitiform papillae, arrangement is rosette shape in *Enigmilichia*, *Leptometopa coquilletti* (Hendel, 1907) (Fig. 45) and *Milichiella*, whereas on an elongate shaft in *Desmometopa* (Fig. 46) and *Milichia*. The posterior spiracles are borne on widely separated dorsal protuberances (Fig. 47) and most lack a peritreme, not on a uniform plate and each consisting of three projections (Figs 48, 49). Each projection has a straight to slightly curved spiracular opening, with conspicuous branching peristigmatic tufts in three or four clumps.

The puparia of eight species are known, based on Ferrar (1987: 226) and Roháček (1995) and the latter noted that male puparia of *Milichiella tiefii* are slightly larger on average than those of females. Puparia range from 2.66–4.20 mm in length and 0.69–1.40 mm in width (Ferrar 1987: 225; Roháček 1995), are yellowish brown to dark reddish brown in colour and are depressed dolioform (*sensu* Clopton 2004) in shape (Fig. 50) (Bohart & Gressitt 1951; Ferrar 1987: 226; Roháček 1995; Papp & Wheeler 1998: 321). The posterior spiracles are visible, as in the larvae. The prothoracic spiracles are obscured in *Leptometopa* and *Phyllomyza*, but are visible in *Desmometopa*, *Enigmilichia*, *Milichia* and *Milichiella* (Deeming & Báez 1985; Ferrar 1987: 226).

Economic significance

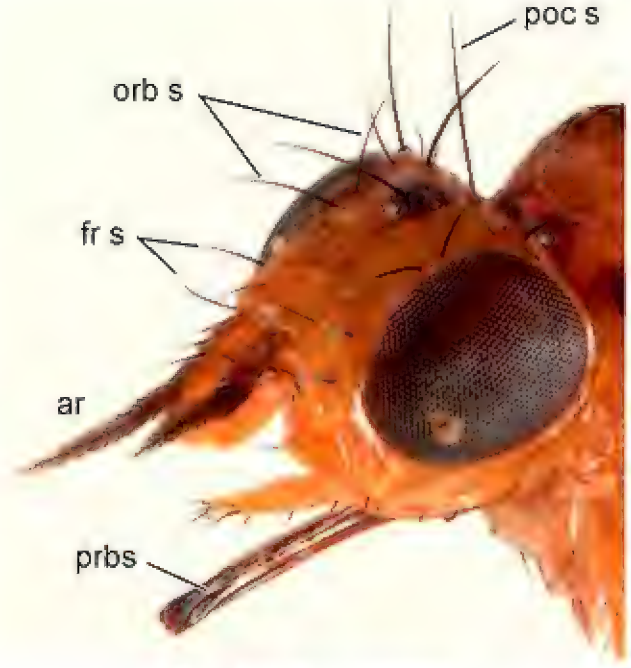
Although milichiids do not have any known appreciable economic impact, Ferrar (1987: 222) indicated that the "filth-fly" biology of several species makes them prone to dispersal by human activities and to be potential vectors of faecal-borne diseases (see also Bohart & Gressitt (1951)). Okaeme (1983) recorded numerous acalyptrate flies, including species of *Desmometopa* and *Leptometopa*, associated with domestic cattle wounds in Nigeria. He indicated that the irritation by these flies could reduce cattle productivity and that flies could serve as mechanical vectors for pathogens. The only documented case of a milichiid having a significant economic impact was *D. varipalpis* Malloch, 1927, infesting the bio-filtration system of a corn processing plant in Indiana, U.S.A. (Williams & Walker 1981); pesticides were required to eradicate the flies. *Desmometopa varipalpis* is considered to be a virtually cosmopolitan species and occurs in the Afrotropics. Zuska & Laštovka (1969) recorded the species *D. sordida* (Fallén, 1820), *Leptometopa latipes* and *Madiza glabra*, all occurring in low populations not requiring control, in food processing plants in the former Czechoslovakia. Of these species, both *D. sordida* and *L. latipes* also occur in the Afrotropics and could occur in similar types of food processing facilities in the region.

Classification

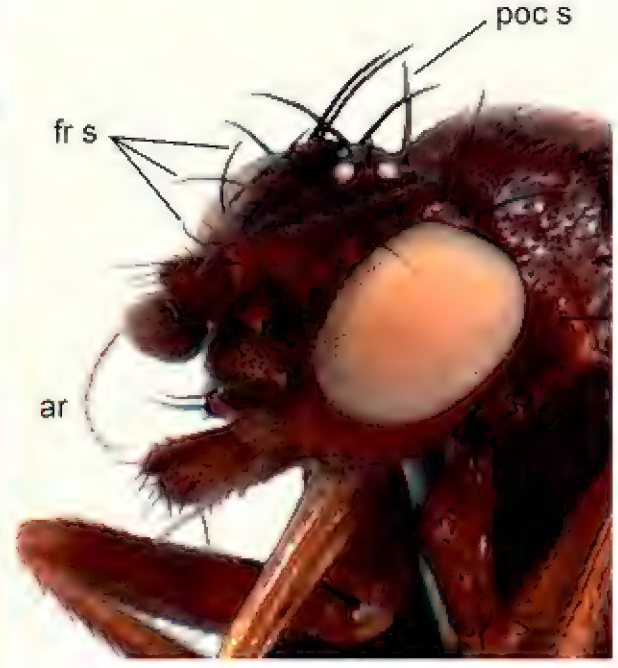
The family-level relationship of Milichiidae to other higher taxa has been somewhat unstable. Griffiths (1972: 220) placed the Milichiidae in his prefamily Tephritoinea, along with other families, including Chloropidae, Tephritidae and Odiniidae. Brake (2000) noted that this prefamily concept is no longer recognised and many of the families within the group were by the year 2000 considered to be in a variety of different superfamilies. Hennig (1973: 60) and McAlpine (1989: 1468) recognised a superfamily including Carnidae, Chloropidae and Milichiidae and in the case of McAlpine, he also included several others, such as non-Afrotropical Risidae and Cryptochetidae. Brake (2000) and Buck (2006) both found Chloropidae

and Milichiidae to be sister-groups, with Brake recovering non-Afrotropical Acartopthalmidae as the sister to Chloropidae + Milichiidae, while Buck found Cryptochetidae to be sister to Chloropidae + Milichiidae. Both of these works were based on morphological characters only and Brake (2000) questioned whether Carnidae also belongs in the superfamily. Wiegmann *et al*. (2011) developed a phylogeny based on molecular data. This work concluded that while Milichiidae + Chloropidae are sister-groups, the nearest related group to them was non-Afrotropical Somatiidae, with Carnidae and Acartophthalmidae well-removed from each other and from Milichiidae + Chloropidae.

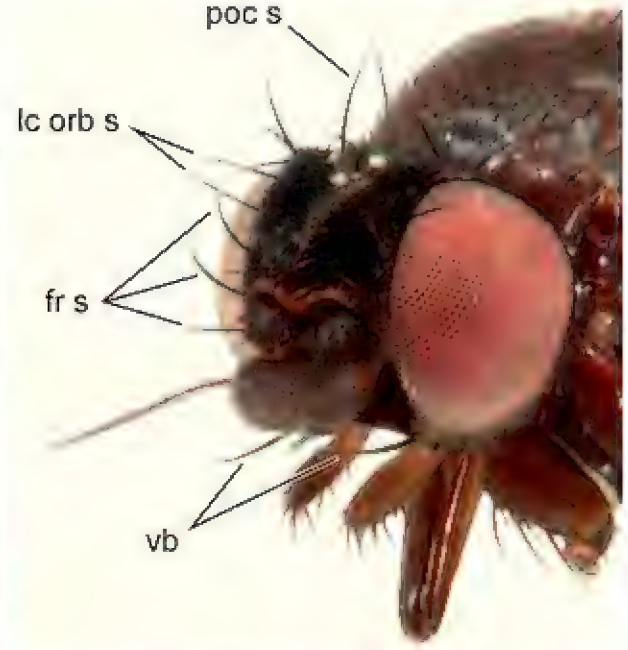
Numerous treatments of the Milichiidae list two subfamilies: Madizinae and Milichiinae (e.g., Papp & Wheeler 1998: 322; Sabrosky 1980: 686, 1987*a*: 904). Brake (2000, 2009) recognised three subfamilies. Besides Milichiinae, she separated Madizinae *sensu lato* into two subfamilies: Madizinae and Phyllomyzinae. Swann (2010: 1127) did not apply subfamilies for several reasons; including that character state distributions of several undescribed genera do not match well with Brake's phylogeny. Several of the undescribed genera could be placed in two different subfamilies each, with other undescribed genera altering the phylogenies within two of Brake's subfamilies. Furthermore, Swann (2010: 1127) noted several of the taxa in Phyllomyzinae had missing data for some of the characters used as synapomorphies for the subfamily. Hennig (1958) argued that Milichiinae are clearly monophyletic, but noted that Madizinae do not have any clear synapomorphy and may be paraphyletic, as later suggested by Brake



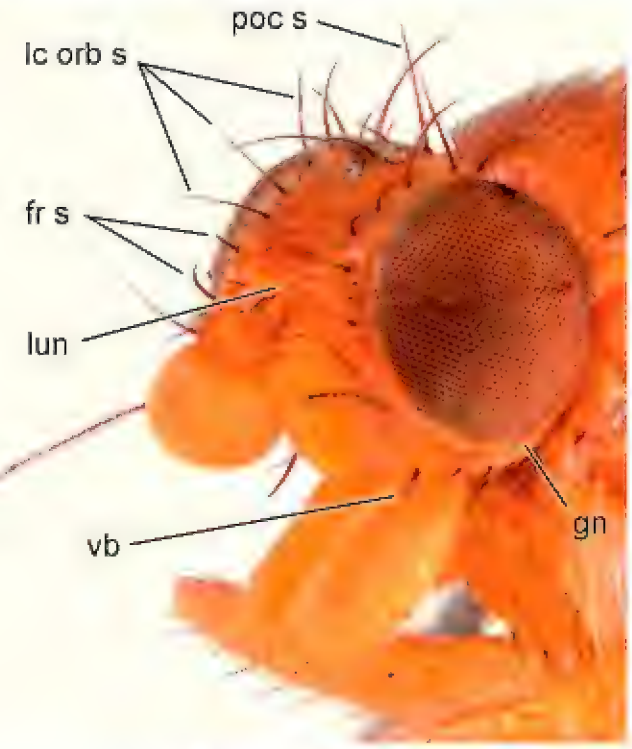
17 *Aldrichiomyza*



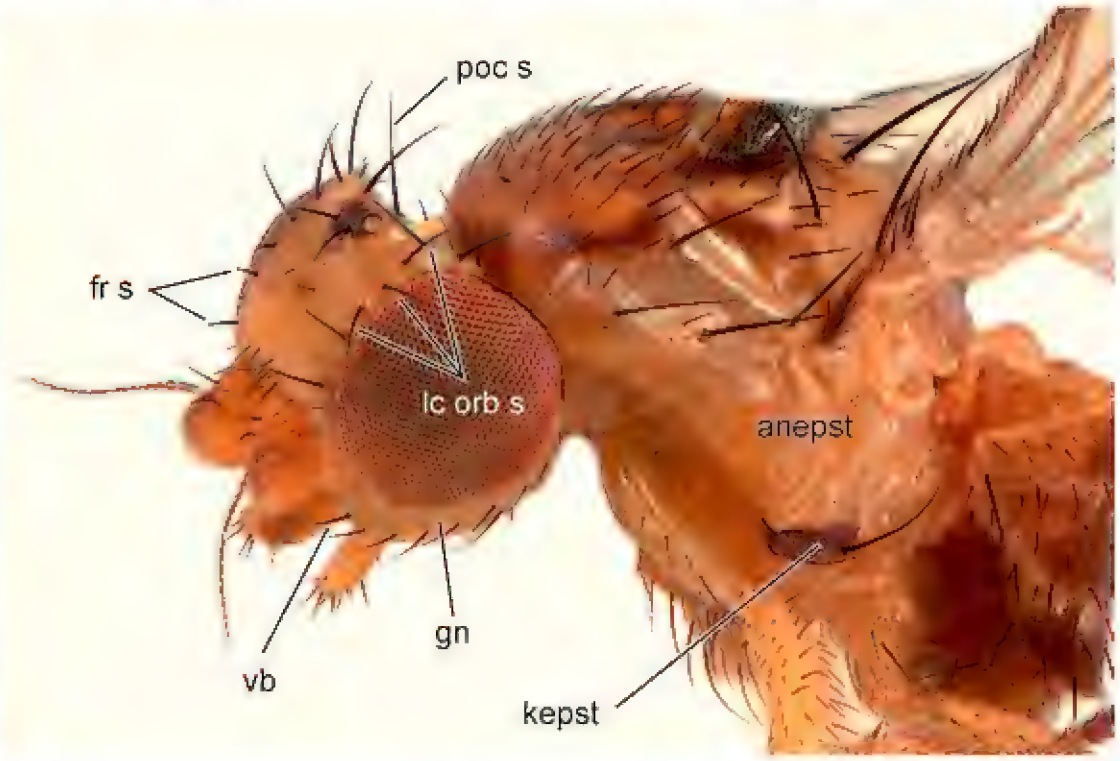
18 *Paramyia*



19 *Neophyllomyza*



20 *Phyllomyza*

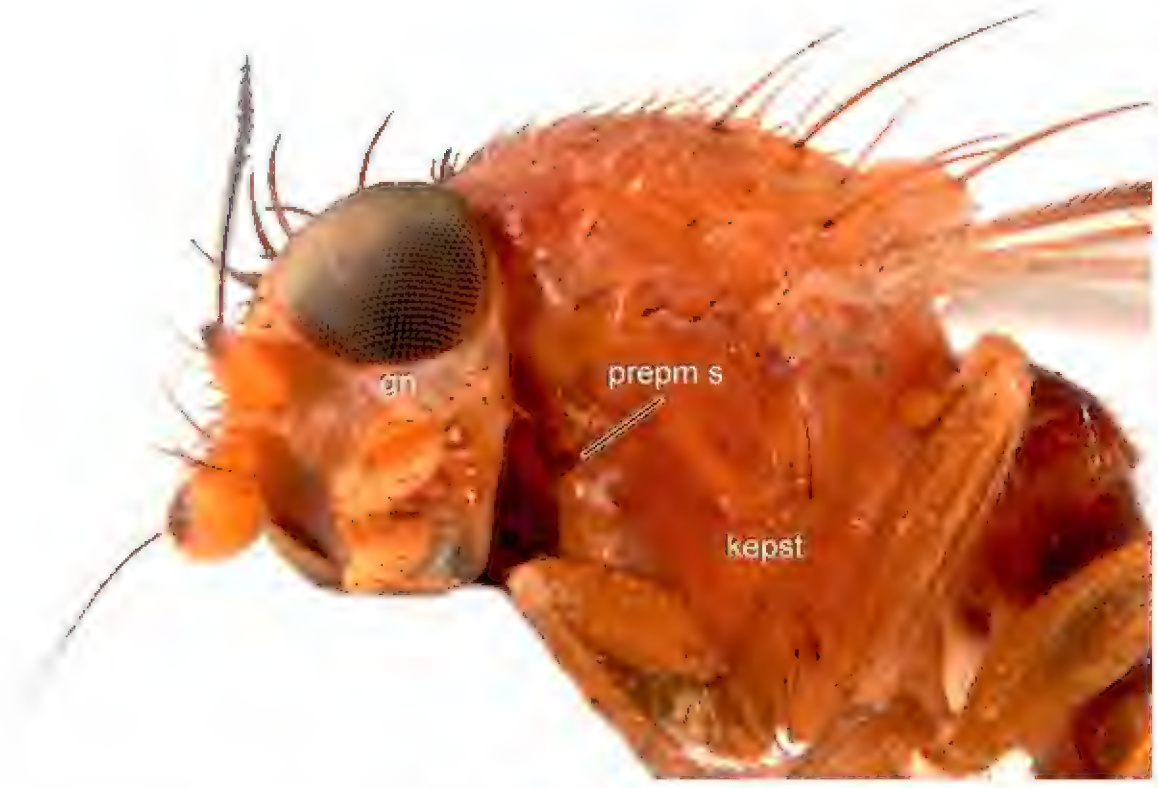


21 *Stomosis*

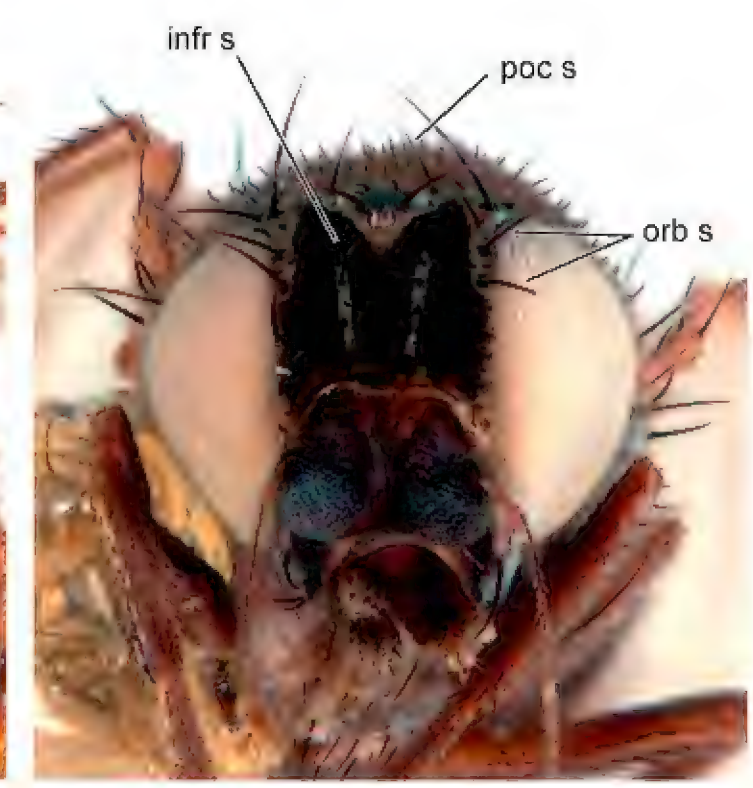
Figs 95.17–21. Heads and heads and thoraces of Milichiidae: (17) head of *Aldrichiomyza* sp., dorsolateral oblique view ♀ (non-Afrotropical); (18) same, *Paramyia* sp. ♀; (19) same, *Neophyllomyza* sp. ♀; (20) same, *Phyllomyza* sp. ♂; (21) head and thorax of *Stomosis* sp., dorsolateral oblique view ♀.

Abbreviations: anepst – anepisternum; ar – arista; fr s – frontal setae; gn – gena; kepst – katepisternum; lc orb s – lateroclinate orbital setae; lun – lunule; orb s – orbital setae; poc s – postocellar seta; prbs – proboscis; vb – vibrissa(e).

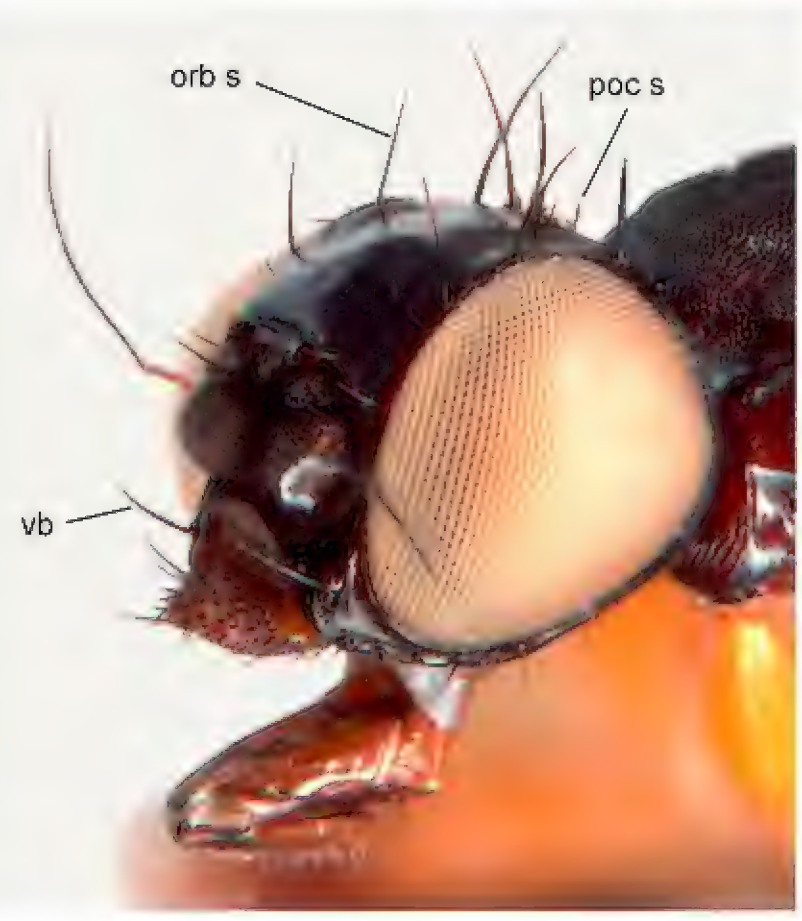
(2000). Furthermore, the use of a relatively distant taxon as outgroup, such as Acartophthalmidae, for polarising characters within the Milichiidae may also cause problems. Having added two undescribed genera into Brake's matrix, filling in some of these missing data from her matrix and then re-analysing these data there were significant changes, including the collapse of her subfamilies Madizinae and Phyllomyzinae into a single clade (Swann, unpubl.). Since there are more than 15 undescribed higher taxa, including those noted in this chapter, which may alter the subfamilies status further or maintain Brake's hypothesised higher phylogeny it is here deferred to Brake's phylogeny of the family, until formal description of genera reveals further morphological diversity in the family. It is attempted to roughly place the undescribed Afrotropical taxa into Brake's subfamilies, based on the synapomorphies noted in the following paragraphs and her use



22 *Phyllomyza*



23 *Desmometopa*

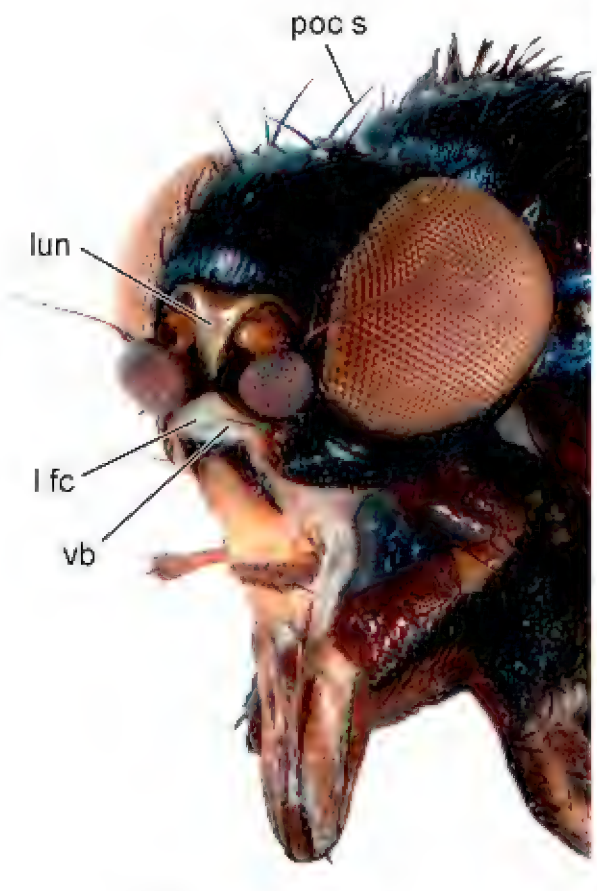


24 *Desmometopa* (*Litometopa*)

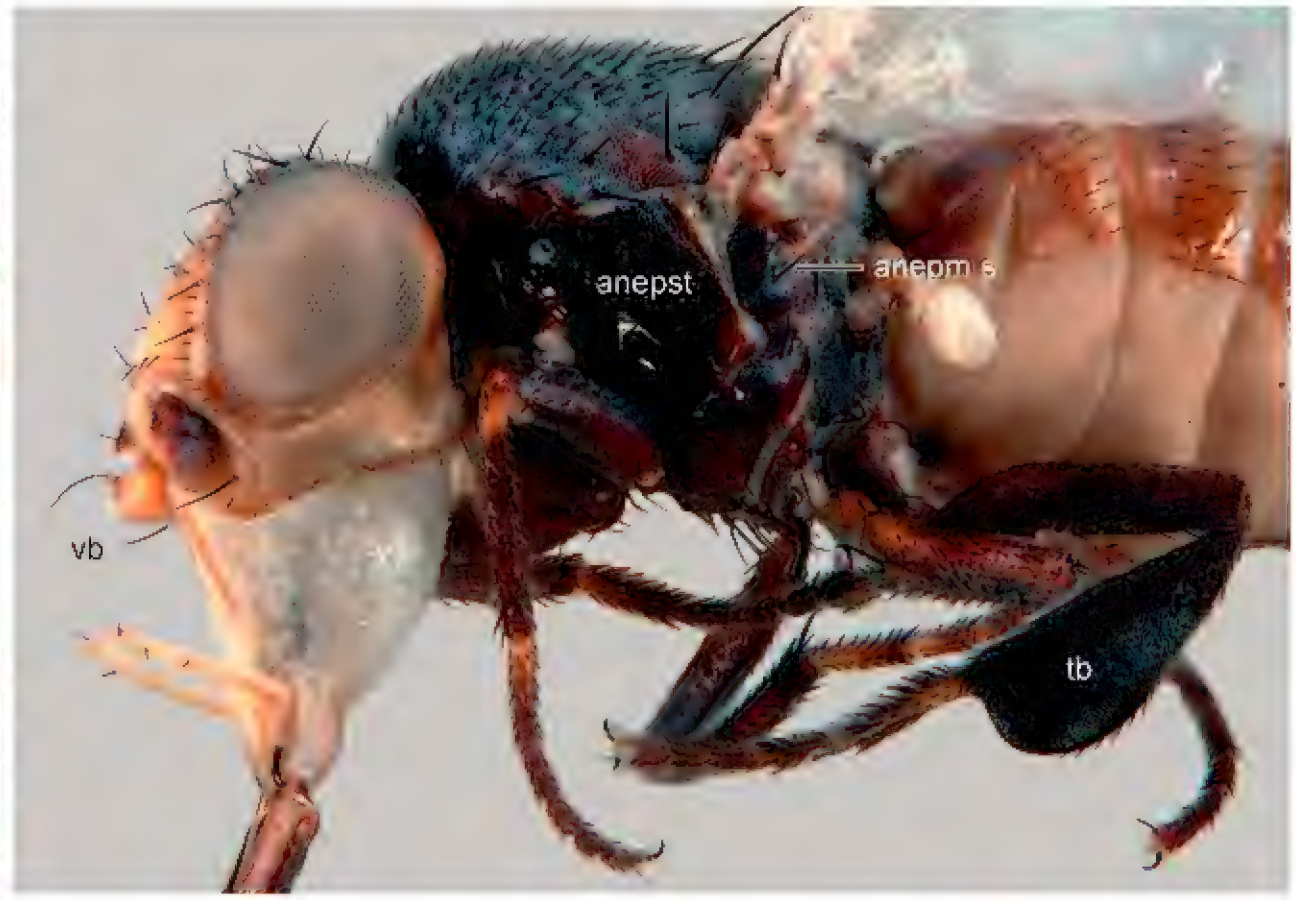
25 *Desmometopa* (*Litometopa*)

Figs 95.22–25. Heads and heads and thoraces of Milichiidae: (22) head and thorax of *Phyllomyza* sp., ventrolateral oblique view ♀; (23) head of *Desmometopa* sp., frontal view ♀; (24) same, *Desmometopa* (*Litometopa*) sp., lateral oblique view ♀; (25) same, head and thorax, lateral view.

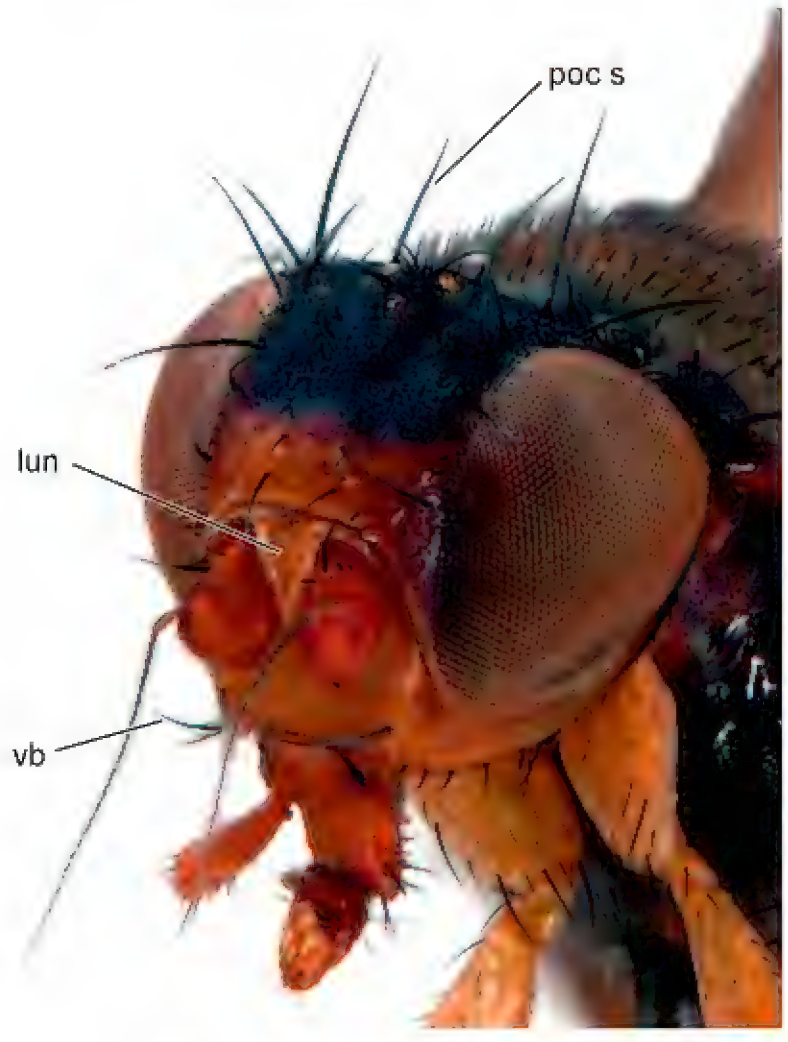
Abbreviations: fem – femur; gn – gena; infr s – interfrontal setae; kepst – katepisternum; orb s – orbital seta(e); poc s – postocellar seta; prepm s – proepimeral seta; vb – vibrissa.



26 *Leptometopa*



27 *Leptometopa*



28 Undescribed genus B

29 Undescribed genus B

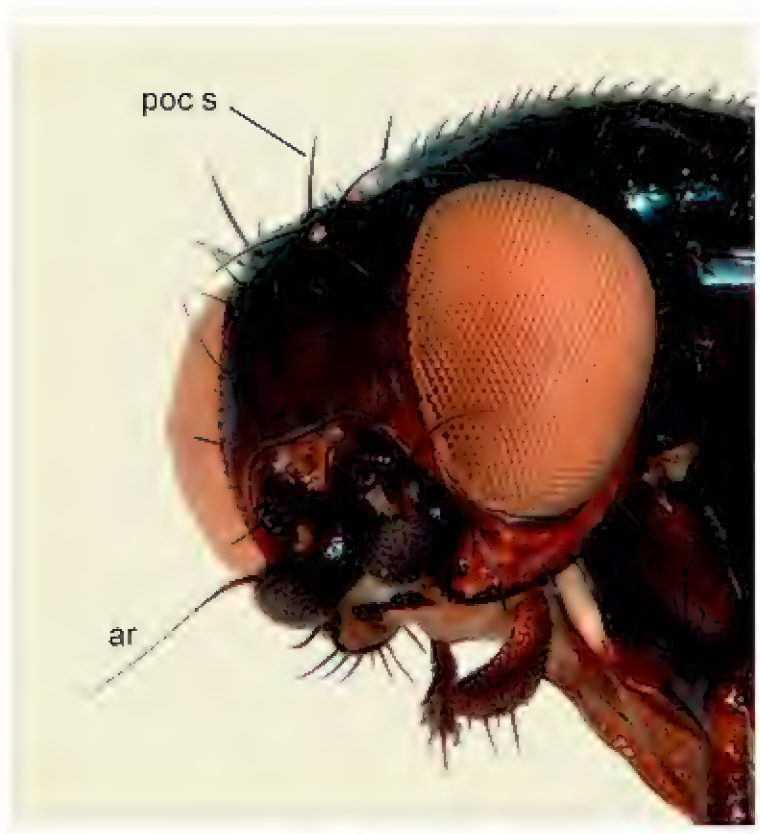
Figs 95.26–29. Heads and heads and thoraces of Milichiidae: (26) head of *Leptometopa* sp., lateral oblique view ♀ (non-Afrotropical); (27) same, head and thorax, lateral view ♂; (28) head of Undescribed genus B, lateral oblique view ♀; (29) same, thorax, lateral view.

Abbreviations: anepm – anepimeron; anepm s – anepimeral seta; anepst – anepisternum; kepst – katepisternum; l fc – lower face; lun – lunule; poc s – postocellar seta; tb – tibia; vb – vibrissa.

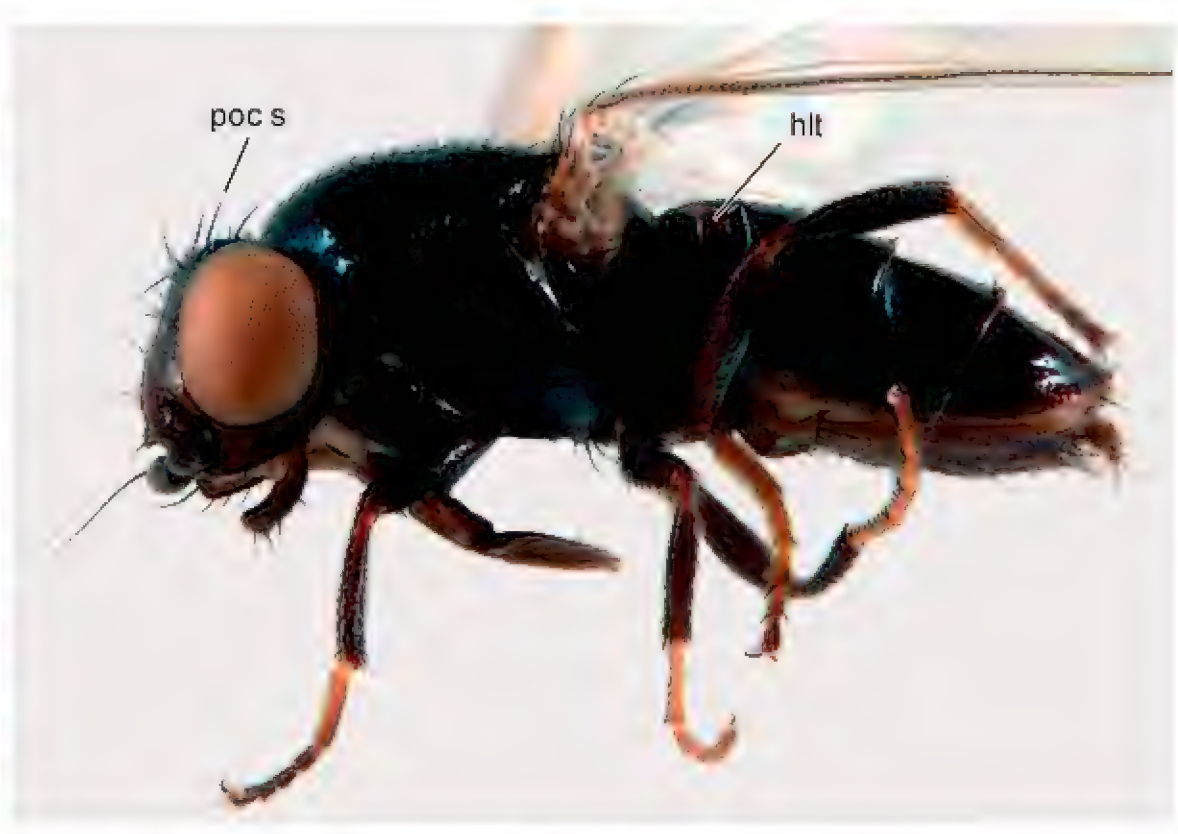
of characters to separate subfamilies applied in her generic identification key.

The subfamily Phyllomyzinae includes the genera *Aldrichiomyza*, *Borneomyia* Brake, *Costalima* Sabrosky, *Microsimus* Aldrich, *Neophyllomyza*, *Paramyia*, *Phyllomyza*, *Stomosis* and *Xenophyllomyza*. The subfamily is defined by the following synapomorphies: two medial pseudotracheae converging at the tips; proepimeral setae present; hind tarsomere 1 with a row of setae; and the ring of barbed spines between segments 7 and 8 in females is lost (Brake 2000). Of these characters, only that of the medial pseudotracheae is unique and does not reverse, however this character was not coded for *Costalima* nor *Microsimus* nor was that of the medial pseudotracheae coded for these two genera.

The subfamily Madizinae (*sensu* Brake 2000; Brake & Friedberg 2003) is comprised of *Desmometopa*, *Leptometopa* and *Madiza*. The Madizinae are characterised by the distiphallus being modified into a membranous tube, which is widened in the middle and by the posterior sclerotised stripe at the base of the distiphallus (Brake 2000). Brake noted that the latter synapomorphy for the subfamily is also present in two genera of Milichiinae and thus may be a plesiomorphy uniting the two subfamilies. Three new genera (Undescribed genus B, Undescribed genus C and Undescribed genus D), are included in

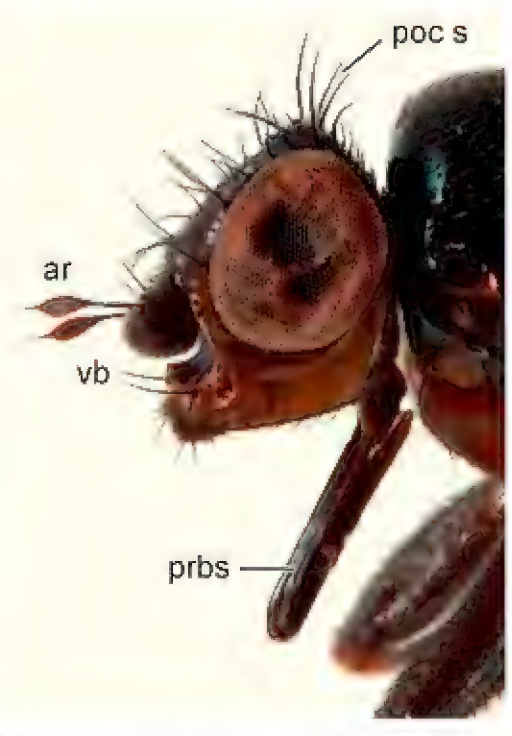


30 *Madiza*

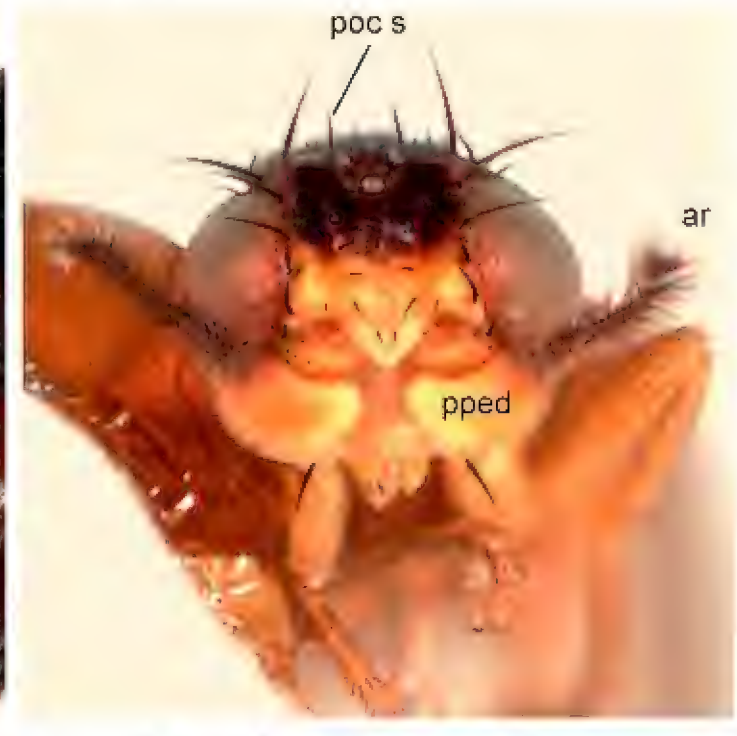


31 *Madiza*

32 Undescribed genus C ♀



33 Undescribed genus C ♂



34 Undescribed genus D ♂

Figs 95.30–34. Heads and habitus of Milichiidae: (30) head of *Madiza* sp., lateral oblique view ♀ (non-Afrotropical); (31) same, habitus, lateral view; (32) head of Undescribed genus C, dorsolateral view ♀; (33) same, lateral view ♂; (34) same, Undescribed genus D, frontal view ♂.

Abbreviations: ar – arista; hlt – halter; poc s – postocellar seta; pped – postpedicel; prbs – proboscis; vb – vibrissa.

this chapter, as all three have postocellar setae that are only slightly converging, or parallel, which is one of the characters Brake (2000) applied in her identification key to separate the subfamily. Deeming (1990) placed Undescribed genus D near *Costalima*, which would place it in the subfamily Phyllomyzinae, but in actuality this may be closer to *Neophyllomyza*, thus its placement in this treatment is for keying convenience only and may not reflect its actual phylogenetic placement.

The subfamily Milichiinae (*sensu* Brake 2000, 2009) includes the genera *Enigmilichia*, *Eusiphona*, *Milichia*, *Milichiella*, *Pholeomyia*, *Pseudomilichia* Becker and *Ulia* Becker. Brake (2000) defines it based on seven synapomorphies of which three: vibrissal angle obsolescent and vibrissa above lower margin of eye; frons in males narrower than in females; and distal margin of anal wing cell (*cua*) meeting vein *CuA+CuP* at a sharp angle, are unique and do not reverse. Undescribed genus A is here placed in this subfamily as it exhibits these synapomorphies.

Identification

With the exceptions of Brake (1999, 2000, 2009) and Brake & Freidberg (2003), there have been no phylogenetic revisions that have closely examined terminalia characters. The only published world generic revisions are those of Brake (2009), Papp (2001*a*) and Sabrosky (1983), but even these include species that were not described, due to insufficient material being available. Sabrosky (1959) is useful along with Becker (1907) for identification keys to some species of *Milichiella* and *Pholeomyia*. Deeming (1976, 1979, 1981) are useful to identify portions of the genus *Milichia*. The only modern world generic identification key is Brake (2000), which will prove problematic for the undescribed Afrotropical fauna. Some species descriptions of Afrotropical taxa are more than 50 years old and are sufficiently vague that species-level identifications are extremely difficult and will probably necessitate examination of types. Milichiidae are best micropinned in the field for later double-mounting (see Chapter 2).

Key to genera of Afrotropical Milichiidae

1. Head with vibrissal angle scarcely evident, if at all; vibrissa inserted well above lower margin of eye (e.g., Figs 2–6, 8) (MILICHIINAE) 2
– Head with vibrissal angle 90° or less, with vibrissa inserted below level of lower margin of eye (e.g., Figs 19–21, 24, 26–28, 31, 33) 6
2. Thorax with anepisternum with 2 or 3 large setae at posterior margin, numerous fine, elongate, scattered setae over remainder of surface and 3 more enlarged setae near anterior margin (Fig. 7); head with 1 pair of posterior reclinate orbital setae, numerous fine, shorter inclinate frontal and orbital setae anterior to reclinate orbital setae (Fig. 6) . . . . . Undescribed genus A
– Thorax with anepisternum with at most single row of enlarged setae at posterior margin, remainder of surface bare (e.g., Figs 3, 5); frontal and orbital setae variable (e.g., Figs 3–5), but never with numerous fine inclinate frontal and orbital setae that are indistinguishable, if frontal and orbital setae similar, then enlarged and reclinate (e.g., Fig. 8) 3
3. Compound eye (Fig. 4), with posterior margin excised at level of antennae, excision narrow, or may continue to lower corner of eye . . . . . *Milichiella* Giglio-Tos
– Compound eye (e.g., Figs 2, 3, 5, 8), with posterior margin not excised at level of antennae 4
4. Thorax with anepisternum with row of strong setae posteriorly (Fig. 5) . . . . . *Pholeomyia* Bilimek
– Thorax with anepisternum bare posteriorly (e.g., Fig. 3) 5
5. Wing with subcostal break not developed into costal lappet; wing oval, with broadly rounded margin to anal region (Fig. 9) . . . . . *Enigmilichia* Deeming
– Wing with subcostal break developed into costal lappet; wing usually triangular, with straight margin to anal region (Fig. 10), sometimes broadly rounded (Fig. 11) . . . . . *Milichia* Meigen
6. Head (e.g., Figs 19–21), with postocellar setae cruciate, or strongly convergent, so that apices of setae nearly meet (PHYLLOMYZINAE) 7
– Head (e.g., Figs 23, 28, 30, 34), with postocellar setae only slightly convergent or parallel (MADIZINAE) 11
7. Costal wing vein (C) extending to vein R_{4+5} (e.g., Figs 12, 13) 8
– Costal wing vein (C) extending to vein M_1 (e.g., Figs 14, 15) 9
8. Wing (Fig. 12), with discal medial crossvein (*dm–m*); head (Fig. 17), with antennal arista thickened at base, densely long-setulose . . . . . *Aldrichiomyza* Hendel
– Wing (Fig. 13), without discal medial crossvein (*dm–m*); head (Fig. 18), with antennal arista slender, pubescent . . . . . *Paramyia* Williston
9. Head (Fig. 19), with frons with 2 pairs of lateroclinate orbital setae; wing (Fig. 14), with discal medial cell (*dm*) short; discal medial crossvein (*dm–m*) 2–3 × as far from wing margin as from radial–medial crossvein (*r–m*) . . . . . *Neophyllomyza* Melander

– Head (e.g., Figs 20, 21), with frons with 3 pairs of lateroclinate orbital setae; wing (e.g., Fig. 15), with discal medial cell (*dm*) long; discal medial crossvein (*dm–m*) *ca* equidistant from wing margin and radial–medial crossvein (*r–m*), or closer to wing margin than to crossvein *r–m*. 10

10. Thorax with proepimeral setae (Fig. 22); head with length of lower margin of gena clearly shorter than greatest length of head (Fig. 22); body colour various, but if orange-yellow, dorsal margin of katepisternum also orange-yellow. . . . . *Phyllomyza* Fallén

– Thorax without proepimeral setae (Fig. 21); head with length of lower margin of gena equal to slightly subequal to greatest length of head (Fig. 21); body colour orange-yellow, with dorsal margin of katepisternum brown (Fig. 21) . . . . . *Stomosis* Melander

11. Head with 1 orbital seta, without interfrontal setae (Fig. 24); legs with fore coxa orange to bright yellow, elongate, combined with rows of strong spines on fore femur, giving fore legs raptorial appearance (Fig. 25). . . . . *Desmometopa* (*Litometopa* Sabrosky)

– Head with orbital and interfrontal setae (e.g., Fig. 23); legs with fore coxa orange-brown, brown or black, rarely elongate; fore femur never with spines. 12

12. Head with frons with 2 rows of interfrontal setae, borne on greyish sclerotised interfrontal strips; interfrontal strips, similarly coloured fronto-orbital plates and ocellar triangle demarcating dull to velvet black M-shaped area (Fig. 23) . . . . . *Desmometopa* Loew [in part]

– Head if with interfrontal setae on frons, then without dull to velvet black M-shaped area (e.g., Figs 26, 28, 30, 32, 34). 13

13. Head with lunule extended ventrally on midline of face as flat plate between antennae, reaching beyond base of postpedicel (e.g., Figs 26, 28) 14

– Head with lunule not extended ventrally on midline of face as flat plate dividing antennae and not extending to base of postpedicel (e.g., Figs 30, 32, 34). 15

14. Head with lunule extended almost to lower margin of face; lower margin of face usually extended dorsally, subtriangular (Fig. 26); thorax with anepimeron usually with short, stout seta; anepisternum usually bare (Fig. 27) . . . . . *Leptometopa* Becker

– Head with lunule not extended to lower margin of face (Fig. 28); lower margin of face not extended dorsally; thorax with anepimeron bare; anepisternum highly setulose (Fig. 29) . . . Undescribed genus B

15. Body colour polished black, sometimes with some orange or brown (e.g., Fig. 31) 16

– Body colour dull or subshiny black, brown or orange. 17

16. Halter brown or black (Fig. 31); head with antennal arista of both sexes thin, not widened (Fig. 30) ("typical" Palaearctic traits). . . . . *Madiza* Fallén [in part]

– Halter orange; head with antennal arista of male broadly hastate (Fig. 33); arista of female slightly widened medially (Fig. 32) . . . . . Undescribed genus C

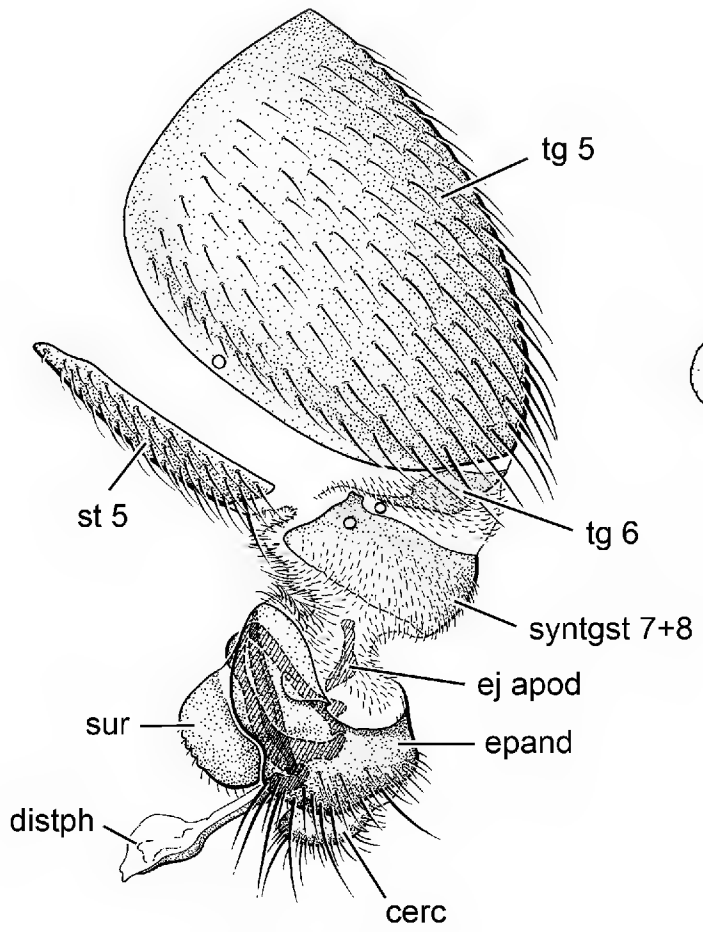
17. Wing (Fig. 16), with long discal medial cell (*dm*); discal medial crossvein (*dm–m*) virtually equidistant from wing margin (along vein M_4) and from crossvein *r–m*; head with antennal arista of male of normal length, not reduced; postpedicel of male unmodified ("atypical" Afrotropical traits) . . . . . *Madiza* Fallén [in part]

– Wing (as in Fig. 14), with short discal medial cell (*dm*); discal medial crossvein (*dm–m*) 2–3 × as far from wing margin as from crossvein *r–m*; head with antennal arista of male greatly reduced; postpedicel of male highly modified on lateral margin into plumose strap-like structure (Fig. 34) . . . . . .Undescribed genus D

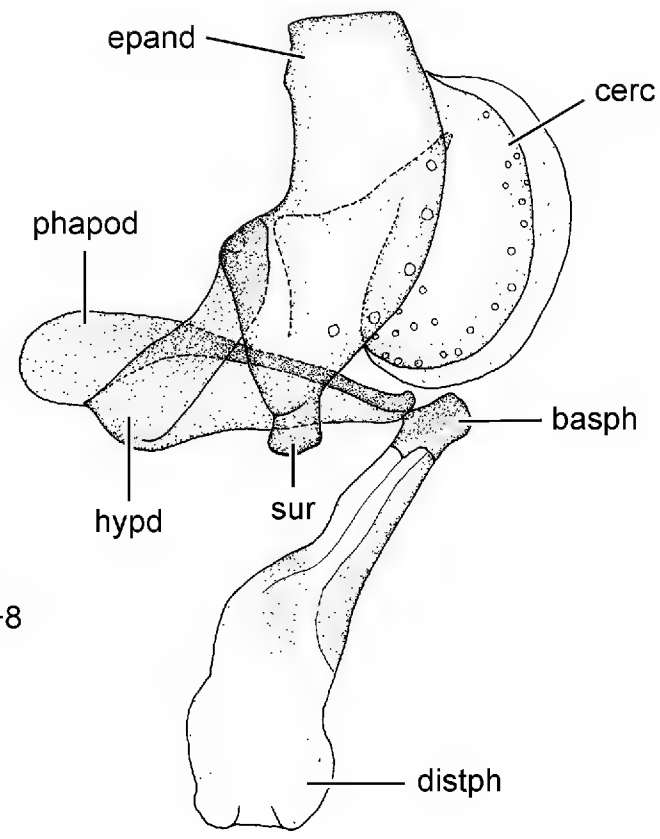
Synopsis of the fauna

The number of described species in most regions of the world, including the Afrotropics, is a serious underestimation of the likely number present. Stork (1991) sampled 169 Milichiidae specimens, comprising 25 species through canopy fogging of Bornean rainforest trees. Swann (2010: 1134) estimated that slightly less than 50% of the Central American fauna was known. Swann (2000: 266) examined 107 specimens, comprising 29 species, of which only two could be confirmed as described species, in a preliminary faunal survey of Namibia. Kirk-Spriggs & Stuckenberg (2009: 185) estimated there may be 192–203+ undescribed species in the Afrotropics. There are currently 77 described species in 11 described genera in the Afrotropics, but an additional 140–150 undescribed species in at least 15 genera should be expected.

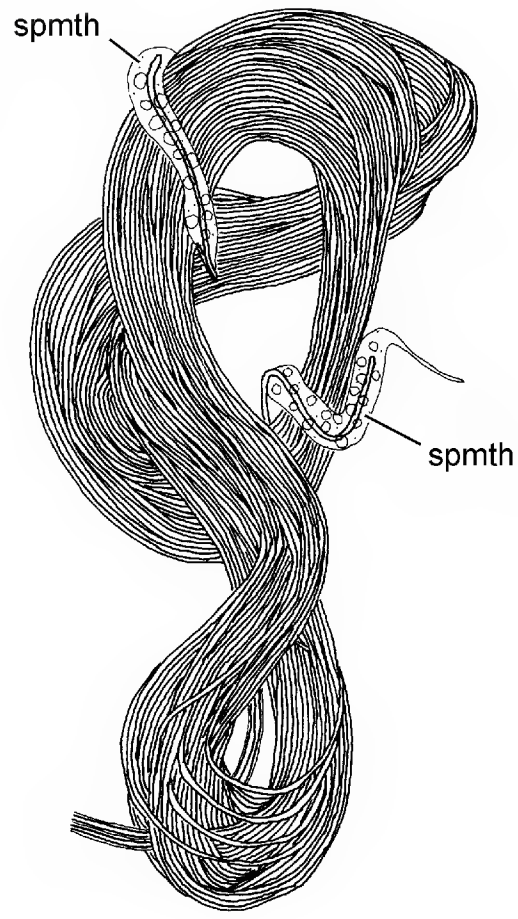
***Aldrichiomyza* Hendel** (Phyllomyzinae)**.** A genus of six described species occurring in the Afrotropical, Nearctic, Oriental and Palaearctic Regions. One species, *A. longirostris* Hendel, 1931, is known to occur in Sudan in the Afrotropics, as well as Palaearctic Egypt and Israel. Swann (2000: 267) noted additional material of the genus from Botswana and since that time further specimens are known from Kenya, Madagascar and Namibia. None of the Southern African material represents described species and all material examined was



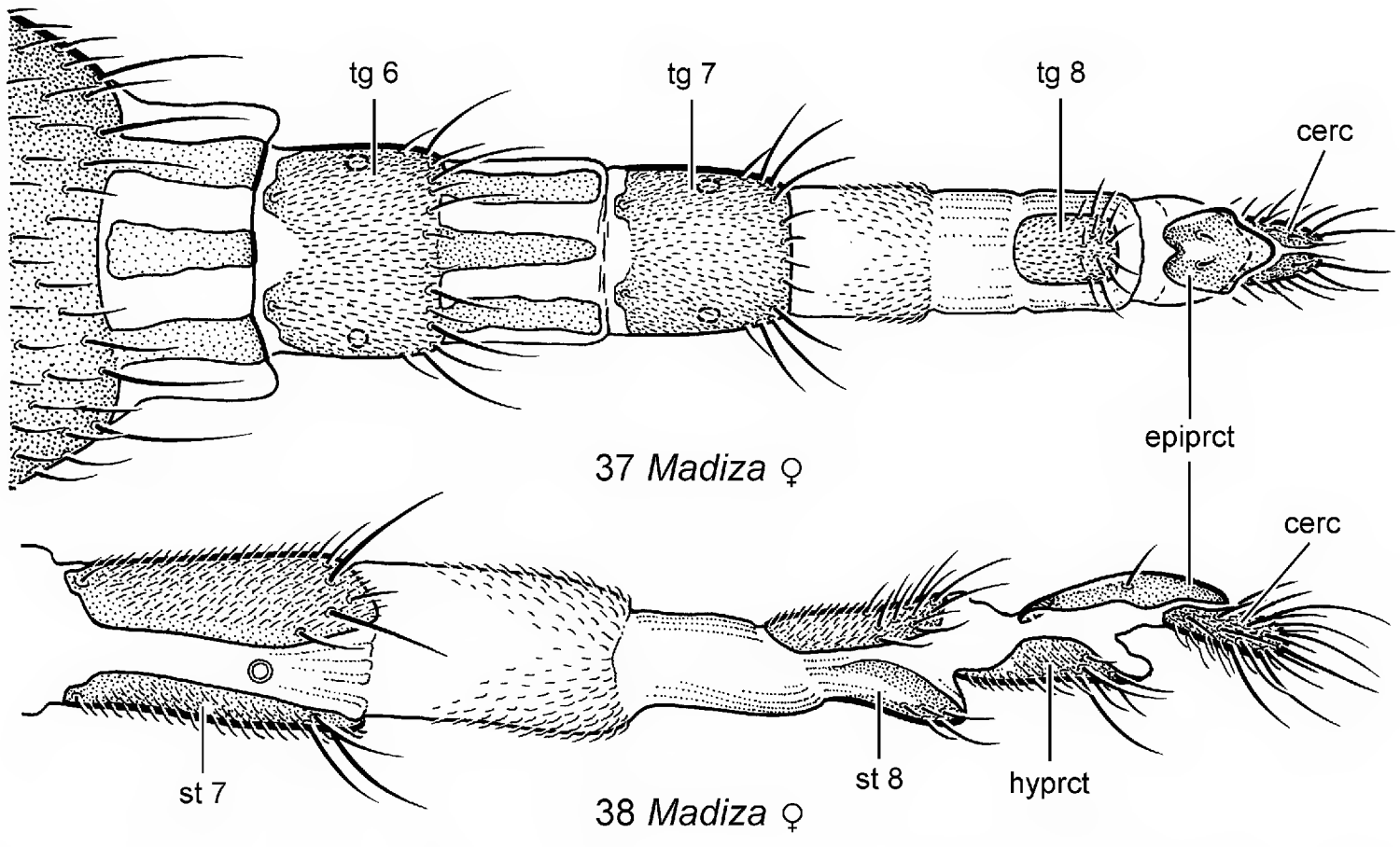
35 *Madiza* ♂



36 *Desmometopa* ♂



39 *Madiza* ♀



37 *Madiza* ♀

38 *Madiza* ♀

Figs 95.35–39. Male terminalia and female postabdomen of Milichiidae: (35) male terminalia of *Madiza glabra* Fallén, lateral view (non-Afrotropical); (36) same, *Desmometopa sordida* (Fallén) (non-Afrotropical); (37) female postabdomen of *M. glabra*, dorsal view; (38) same, lateral view; (39) same, spermathecae. Figs 35, 37, 38 (after Sabrosky 1987*a*, figs 11, 9, 8, respectively), Figs 36, 39 (after Brake 2000, 13A, 24E).

Abbreviations: basph – basiphallus; cerc – cercus; distph – distiphallus; ej apod – ejaculatory apodeme; epand – epandrium; epiprct – epiproct; hypd – hypandrium; hyprct – hypoproct; phapod – phallapodeme; spmth – spermatheca; st – sternite; sur – surstylus; syntgst – syntergosternite; tg – tergite.

collected seasonally between December and February. There are probably three or four undescribed species in the Afrotropics. The genus is readily distinguished by the densely long-setulose antennal arista with a thickened base (Fig. 17), the cruciate postocellar setae (Fig. 17) and the costal wing vein (C) extending to vein R_{4+5} (Fig. 12). There appears to be little biological information for the genus, except that the Oriental species *A. flaviventris* Iwasa, 1997, was collected on shrubs around rotting prawns, being used to attract saprophagous flies (Iwasa 1997) and the immature stages remain unknown. This may indicate a general saprophagous habit for the genus. All specimens from Botswana and Namibia were collected in Malaise traps. With the exception of *A. iwasa* Papp, 2006, the described species can be identified using the identification keys provided by Hendel (1931) and Papp (2001*b*).

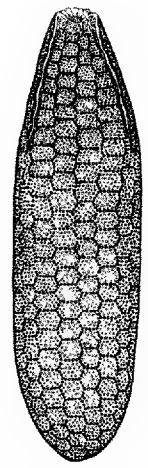
***Desmometopa* Loew** (Madizinae)**.** A genus of 51 described species occurring in all zoogeographical regions, except Antarctica (Sabrosky 1983). Twenty-one described species occur in the Afrotropics, divided into three subgenera: *D.* (*Platophrymyia* Williston), with one described Afrotropical species, *D.* (*P.*) *nigeriae* Sabrosky, 1983, described from Nigeria; *Desmometopa sensu stricto* with 13 Afrotropical species (Brake 2000); and *D.* (*Litometopa* Sabrosky), which comprises seven endemic Afrotropical species (Brake & Freidberg 2003). Given that the subgenus *D.* (*Platophrymyia*) is primarily New World, it is unlikely that there are more than one or two undescribed species in the region, but there are likely 8–10 undescribed species in the subgenus *Desmometopa sensu stricto*. There appears to be a general paucity of records from the northern Afrotropics (Burkina Faso, Chad, Mali, Mauritania and Niger) and from Southern African countries (Angola, Botswana, Mozambique, Zambia and Zimbabwe), which is likely an artefact of collecting effort. Single specimens of two undescribed species of *D.* (*Litometopa*) are known from Ghana and Sierra Leone and there are probably at least five undescribed species in the subgenus. This genus is readily distinguished by the two rows of interfrontal setae (Fig. 23), borne on greyish sclerotised interfrontal strips, which together with similarly coloured frontoorbital plates and ocellar triangle demarcate a dull to velvet black M-shaped area (Fig. 23). Biology of the genus was summarised by Sabrosky (1983) and immature stages have been described (see above). Species of *Desmometopa sensu stricto* and *D.* (*Platophrymyia*) can be identified using the identification keys provided by Sabrosky (1983) and for *D.* (*Litometopa*) by Brake & Freidberg (2003).

***Enigmilichia* Deeming** (Milichiinae)**.** Currently a monotypic genus, with the single species, *E. dimorphica* Deeming, 1981, described from Nigeria and later recorded from Seychelles by Gerlach (2009: 340). Swann (2000: 267) noted additional specimens of *Engimilichia* from Botswana, Burkina Faso and Côte d'Ivoire and further material of the genus has been examined from Ghana, Madagascar, Namibia, South Africa and Zambia, including at least four undescribed species. Brake (2010) recorded a single male specimen of an apparently undescribed species from Greece, thus the genus is both Palaearctic and Afrotropical. The genus is distinguished by its oval wing, the subcostal break not developed into a costal lappet (Fig. 9) and the reclinate orbital and frontal setae. The type species was reared from rotten yam tubers and immature features have been described from puparia (Deeming 1981).

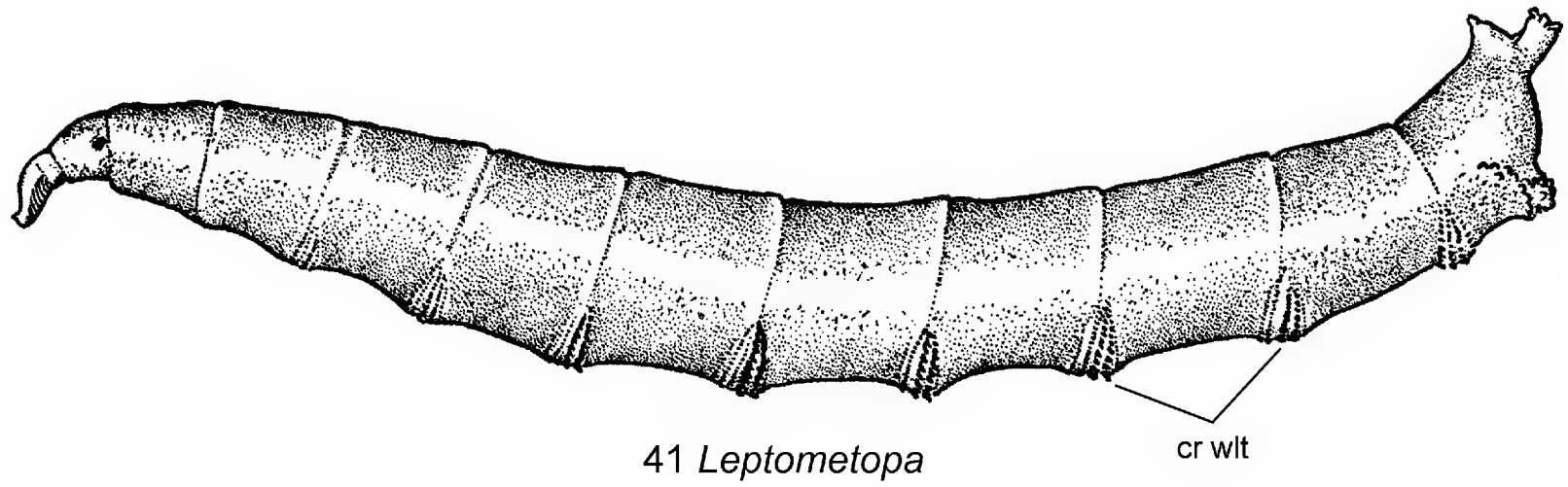
***Leptometopa* Becker** (Madizinae)**.** A genus of 18 described species occurring in all zoogeographical regions, except Antarctica. Seven species are recorded from Comoros, Madagascar, Namibia, Nigeria, Oman, Seychelles, South Africa, Sudan and Yemen (Brake 2009; Deeming 1998: 151) and further material of the genus has been examined from Burkina Faso, Côte d'Ivoire, Ghana and Kenya. Swann (2000: 266) noted at least four species from Namibia that could not be identified to known species and there are at least eight undescribed Afrotropical species. The genus is distinguished by the parallel postocellar setae (Fig. 26), the lunule extended ventrally as a flat plate between the antennae, reaching almost to the lower margin of face, the lower margin of the face usually extended dorsally (Fig. 26), the bare anepisternum (Fig. 27), the anepimeron usually with short, stout seta and the male hind tibia sometimes greatly broadened (Fig. 27). Adults are kleptoparasitic on a range of predaceous arthropods and are found on flowers. *Leptometopa* are known to breed in birds' nests and are associated with bat guano (see above). The larvae of the Afrotropical species, *L. coquilletti*, have been described (Hennig 1956). There is currently no recent identification key to all described Afrotropical species, but Deeming (1998: 148) keyed four Afrotropical and one Palaearctic species.

***Madiza* Fallén** (Madizinae)**.** A genus of six described species occurring in the Afrotropical, Nearctic and Palaearctic Regions. The genus is usually distinguished from other madizines by the black polished body (Fig. 31), the slender antennal arista (Fig. 30), absence of interfrontal stripes, the lunule not extending beyond the pedicel and the hind tibia with an elongate posterior organ in both sexes. The single Afrotropical species, *M. africana* Brake & Papp, 2009, was described from Tanzania, but there is some doubt as to its generic placement (absence of hind tibial organ and dark grey micro-tomentose body) and the species may belong in a separate genus. There are unlikely to be many additional undescribed species of the genus in the Afrotropics and these probably occur in countries bordering the Palaearctic. In the above generic identification key, the term "typical Palaearctic traits" and the "atypical Afrotropical traits" are used, and as such, the genus keys out in two places. The larvae of *Madiza* are coprophagous, occurring on dung and the egg stage has been described and illustrated (Brake 2000; Pape & Wheeler 1998: 318). The Afrotropical species can be identified using a combination of Brake (2007), Brake & Papp (2009) and Papp (1993).

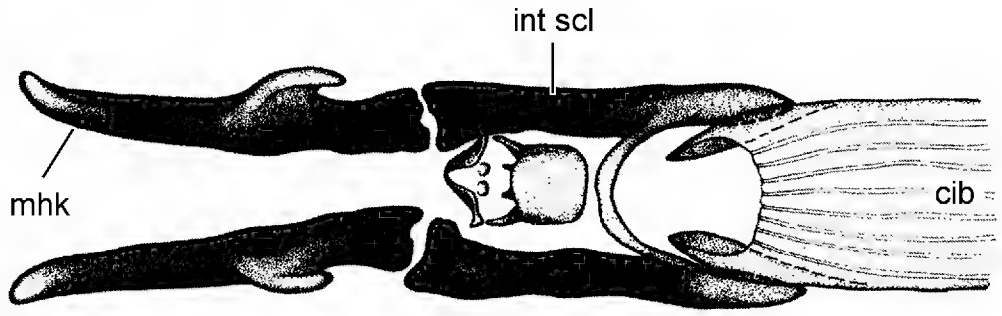
***Milichia* Meigen** (Milichiinae)**.** A genus of 39 described species, occurring in all zoogeographical regions, except Antarctica. Twenty-one described species occur in the Afrotropics, and is widely distributed, including records from Seychelles and Yemen and Oman in the Southern Arabian Peninsula. The genus is distinguished from other milichiines by the posterior margin of the eye being entire, the bare anepisternum (Fig. 3) and the elongate wing, with distinct costal lappet (Figs 10, 11). The *M. distinctipennis* species-group (Brake 2000) is solely Afrotropical, with four described species, known from Cameroon, Côte d'Ivoire, Ghana, Malawi, Nigeria, Republic of Congo, Tanzania and Uganda, but additional specimens have been examined from Angola, Democratic Republic of Congo and Kenya and there are at least 3–5 undescribed species in this species-group. The described species of this group may be identified using Deeming (1981). The remaining 17 described



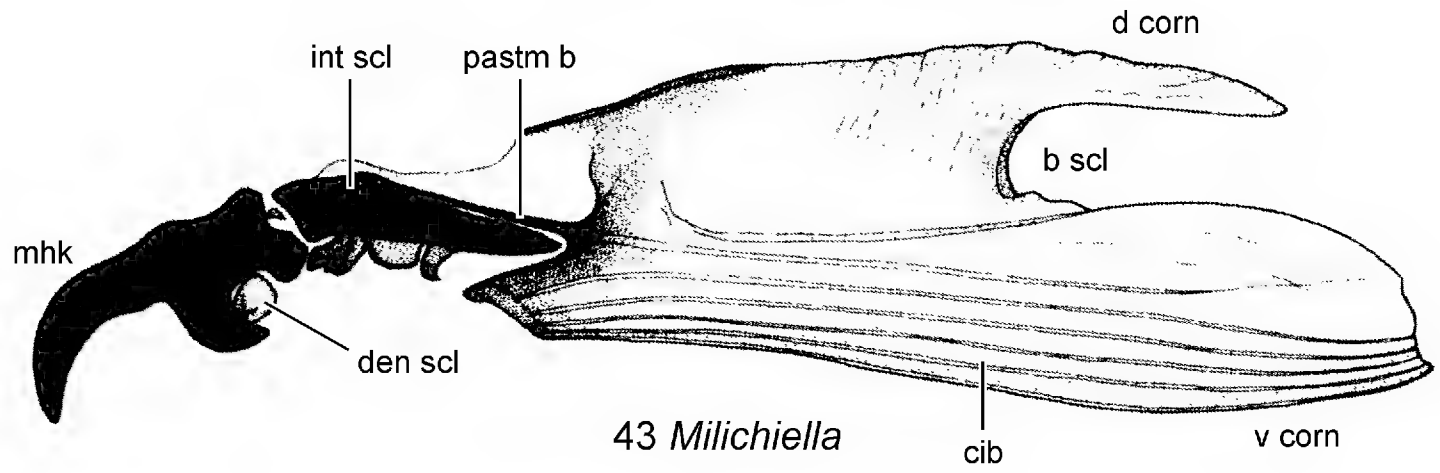
40 *Milichiella*



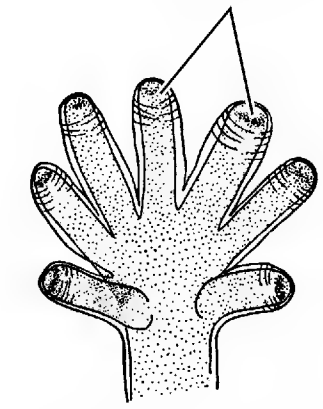
41 *Leptometopa*



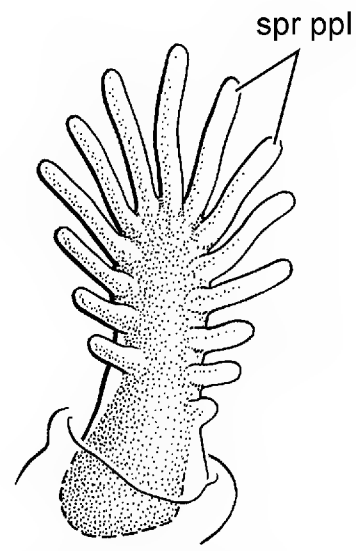
42 *Milichiella*



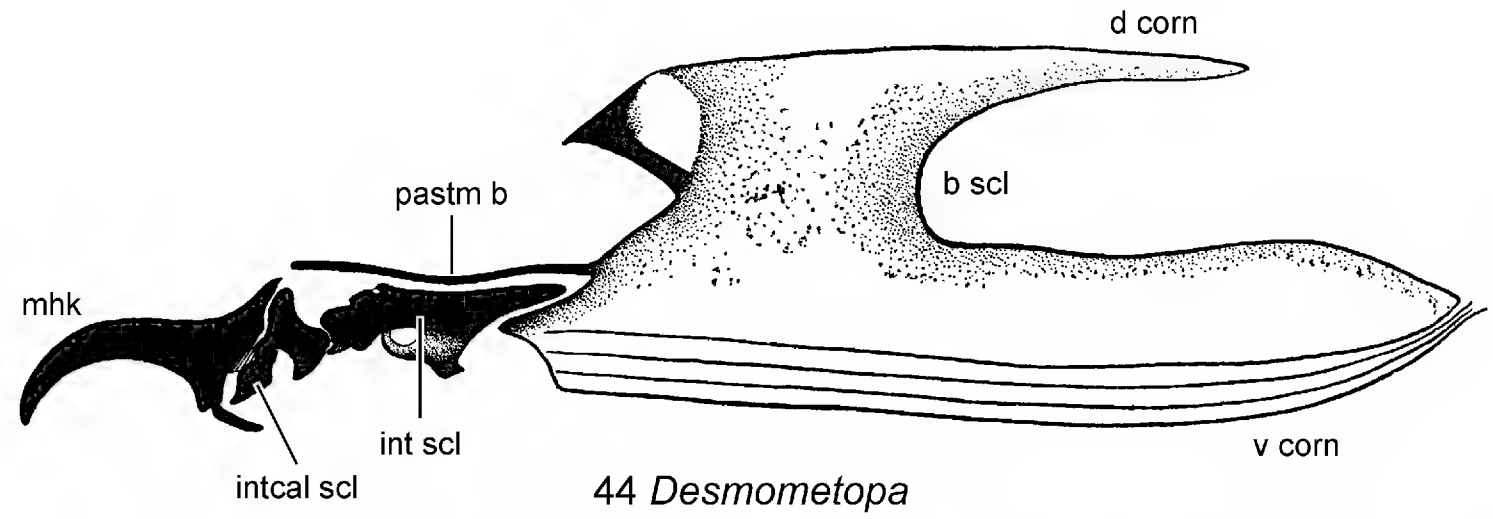
43 *Milichiella*



45 *Leptometopa*



46 *Desmometopa*



44 *Desmometopa*

Figs 95.40–46. Immature stages of Milichiidae: (40) egg of *Milichiella tiefii* (Mik), dorsal view (non-Afrotropical); (41) larval habitus of *Leptometopa coquilletti* (Hendel), lateral view; (42) anterior portion of cephaloskeleton of *M. tiefii*, ventral view; (43) same, cephaloskeleton, lateral view; (44) same, *Desmometopa* sp.; (45) prothoracic spiracle of *L. coquilletti*, lateral view; (46) same, *D. m-nigrum* (Zetterstedt). Figs 40, 42, 43 (Roháček 1995, figs 4, 9, 8, respectively), Figs 41, 44, 45 (Hennig 1956, figs 1A, 4B, 6A), Fig. 46 (Sabrosky 1987*a*, fig. 19).

Abbreviations: b scl – basal sclerite; cib – cibarium; cr wlt – creeping welts; d corn – dorsal cornu; den scl – dental sclerite; int scl – intermediate sclerite; intcal scl – intercalary sclerite; mhk – mouthhook; pastm b – parastomal bar; spr ppl – spiracular papillae; v corn – ventral cornu.

species of *Milichia* lack a cohesive key and require one to consult the original species descriptions for identifications. Swann (2000: 266) noted five undetermined, probably undescribed, species from Namibia and there are no known described species from Namibia. Since then undetermined material has been examined from Burkina Faso, Cameroon and Ghana; all countries with no records of *Milichia*. There are likely at least 18 undescribed species of Afrotropical *Milichia*, in addition to those noted for the *M. distinctipennis* species-group. Adult behaviours have been described for several species (see above) and the immature features have been described from puparia reared from latrines (Deeming & Báez 1985).

***Milichiella* Giglio-Tos** (Milichiinae)**.** A genus of 110 described and named, extant species, occurring in all zoogeographical regions, except Antarctica. Twenty-one extant named species occur in the Afrotropical Region, distributed widely in the continental Afrotropics, in the Indian Ocean islands of Madagascar, Mauritius and Seychelles and in Oman and Yemen in the Arabian Peninsula (Brake 2009; Deeming 1998: 154). Swann (2000: 266) noted a large number of species that occur in Namibia and no material from Namibia was listed by Brake (2009). Other *Milichiella* material has been examined from Botswana and Côte d'Ivoire with no country records listed in Brake (2009) and there are no records from northern Afrotropical countries (Burkina Faso, Chad, Ethiopia, Mali, Mauritania, Niger, Somalia and Sudan), which may be a collecting artefact. At least 6–8 additional undescribed species of *Milichiella* are expected to occur in the Afrotropics. The genus is distinguished from other milichiines, by the presence of a notch or emargination at the posterior margin of the eye (Fig. 4) and by the bare anepisternum (as in Fig. 3). Adults have been collected in caves and the immature stages are known for some extralimital species and reviewed by Brake (2009). The genus was revised on a global basis by Brake (2009), who included an identification key to males of world species, noting that females are unknown for many and are difficult to sort in those species for which they are known.

***Neophyllomyza* Melander** (Phyllomyzinae)**.** A genus of 16 described species, occurring in all zoogeographical regions, except Antarctica. This genus is distinguished by the presence of only two lateroclinate orbital setae (Fig. 19) and by wing cell *dm* short, with crossvein *dm–m* 2–3 × as far from wing margin as from crossvein *r–m* (Fig. 14). Two species are recorded from the Afrotropics: *N. approximatonervis* (Lamb, 1914), described from Seychelles; and *N. inimical* Séguy, 1938, described from Kenya. Swann (2010: 1134) noted that there is a large number of undescribed Neotropical species and the same holds true in the Afrotropics. At least five undescribed species are known from Ghana, Liberia and South Africa and the genus is probably widespread in the continental Afrotropics, with at least eight undescribed species overall. Brochu & Wheeler (2009) noted that the Nearctic species and one Palaearctic species appear to be saproxylic as larvae and the genus as a whole appears to be relatively rare in collections. The genus has been well-sampled in the Nearctic and Oriental Regions, using Malaise and pan traps and virtually all specimens available from Ghana and Liberia were collected in this way. Biology and immature stages otherwise remain unknown. There is currently no satisfactory identification key to the two described Afrotropical species and the genus is in need of revision.

***Paramyia* Williston** (Phyllomyzinae)**.** A genus of 28 described species occurring in the Afrotropical, Nearctic, Neotropical, Oriental and Palaearctic Regions. A single described species occurs in the Afrotropics, *P. africana* Papp, 2001, described from Republic of Congo, but Sabrosky (1980: 687) further listed an unidentified species from Zimbabwe. At least three undescribed species are known for material sampled in Burundi, Democratic Republic of Congo, Ghana, Kenya, Liberia and Madagascar. The genus is probably widespread throughout the Afrotropics, with at least five or six species awaiting description. The genus is readily distinguished by the absence of crossvein *dm–m* and the costal wing vein (*C*) extending to vein R_{4+5} (Fig. 13). Marshall (2019) detailed the phoretic and kleptoparasitic behaviour of an undescribed species of *Paramyia* from Indonesia. The immature stages remain unknown. Papp (2001*a*) provided an identification key to all species known at that time and recently a key to North American species was provided in a revision by Levesque-Beaudin & Mlynarek (2020).

***Pholeomyia* Bilimek** (Milichiinae)**.** A genus of 39 species occurring in the Afrotropical, Nearctic and Neotropical Regions (Brake 2000). A single species, *Pho. politifacies* Sabrosky, 1959, is known from the Afrotropics, recorded from Cameroon, Côte d'Ivoire, Ghana, Nigeria and Uganda. There is very little material of the genus from the Afrotropics in major entomological collections and there are probably only two or three undescribed Afrotropical species. The genus is distinguished from other milichiines by the row of strong setae on the anepisternum, the presence of three orbital and usually three frontal setae (Fig. 5) and the male abdominal tergites are often with silvery pruinescence. *Pholeomyia* are generally associated with decaying vegetable or animal matter and the third-instar larva and puparium have been described for *P. comans* Sabrosky, 1959 (Moser & Neff 1971). The single Afrotropical species can be identified by reference to Sabrosky (1959).

***Phyllomyza* Fallén** (Phyllomyzinae)**.** A genus of 56 extant described species, occurring in all zoogeographical regions, except the Australasian Region and Antarctica. A single species, *P. fuscogrisea* (Séguy, 1933), was described from Mozambique in the Afrotropical Region. At least 60 undescribed species are known from the Afrotropics and this total is similar to the numbers of undescribed species known for other tropical regions. Species of *Phyllomyza* are the most common Milichiidae in Malaise trap samples. The genus is distinguished by the presence of three lateroclinate orbital setae and the male palpus and postpedicel are often enlarged (Fig. 20). Adult behaviours are described above and the puparium for two species have been illustrated (Ferrar 1987: 225; Hennig 1937). The genus is in need of revision and no identification key is currently available.

***Stomosis* Melander** (Phyllomyzinae)**.** A genus of six described species occurring in the Afrotropical, Australasian, Nearctic and Neotropical Regions. Brake & Tschirnhaus (2010) and Swann (2010: 1135) noted numerous undescribed species from the Australasian and Neotropical Regions, respectively and undescribed species are also known from the Oriental Region. Sabrosky (1980: 688) noted an unidentified species from Nigeria and several undescribed species are known from Ghana, Kenya, Liberia, Namibia and South Africa. The genus is probably widespread throughout the continental Afrotropics, with at least six species awaiting description. The genus

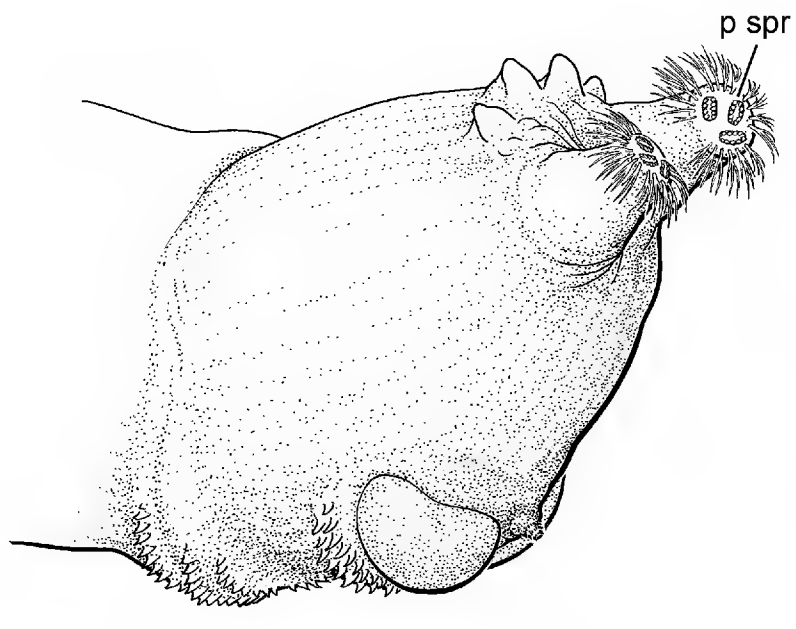
is distinguished by three lateroclinate orbital setae (Fig. 21), the elongate, slender labellum and the usually orange-yellow coloured body, with the dorsal margin of the katepisternum brown. Adults of *S. flava* Sabrosky, 1958 have been reared from puparia collected in tree cavities and kleptoparasitic behaviour has been observed (Brake & Tschirnhaus 2010). The immature stages remain undescribed. The genus is in need of revision and no identification key is currently available.

Undescribed genus A (Milichiinae)**.** This genus is known from a single male specimen collected in the eastern part of Democratic Republic of the Congo. It has a unique combination of traits, including a broad frons with a long series of inclinate frontal and orbital setae, greatly enlarged orbital setae (Fig. 6), numerous anterior and posterior anepisternal setae (Fig. 7) and the costagial break in the wing not forming a costal lappet. Biology and immature stages remain unknown.

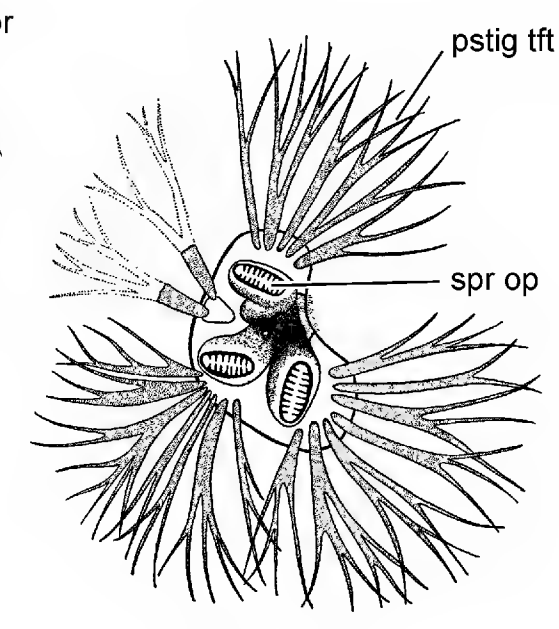
Undescribed genus B (Madizinae)**.** This genus is only known from female specimens from Madagascar and Kenya. The genus is distinguished by the parallel to divergent postocellar setae, the lunule extended ventrally as a flat plate between the antennae, reaching almost to the lower margin of the face (Fig. 28), the lower margin of face not extended dorsally, the anepisternum setose and the anepimeron bare (Fig. 29). Biology and immature stages remain unknown.

Undescribed genus C (Madizinae)**.** This undescribed genus is known from a single collecting event as a large swarm of flies associated with Rock hyrax urine/dung on a seep face in the Western Cape Province, South Africa; otherwise biology and immature stages remain unknown. The genus is distinguished from other madizines by the polished black body, the orange halter and the head with the antennal arista of the male broadly hastate (Fig. 33), whereas the arista of the female is slightly widened medially (Fig. 32). It is unknown how widespread this genus might be in the Afrotropics.

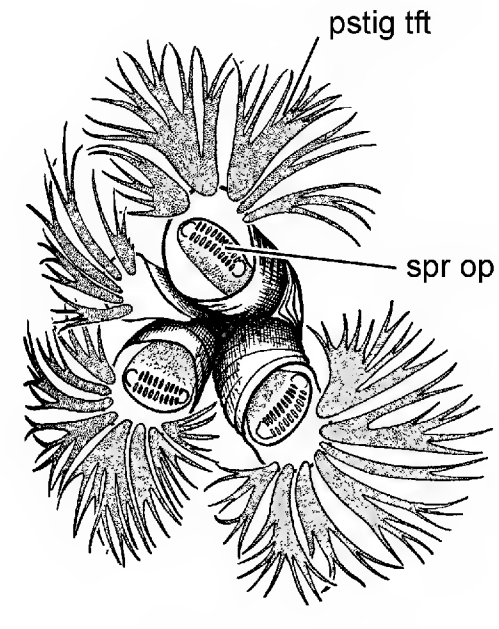
Undescribed genus D (Madizinae)**.** This undescribed genus was first noted by Deeming (1990) and is only known from



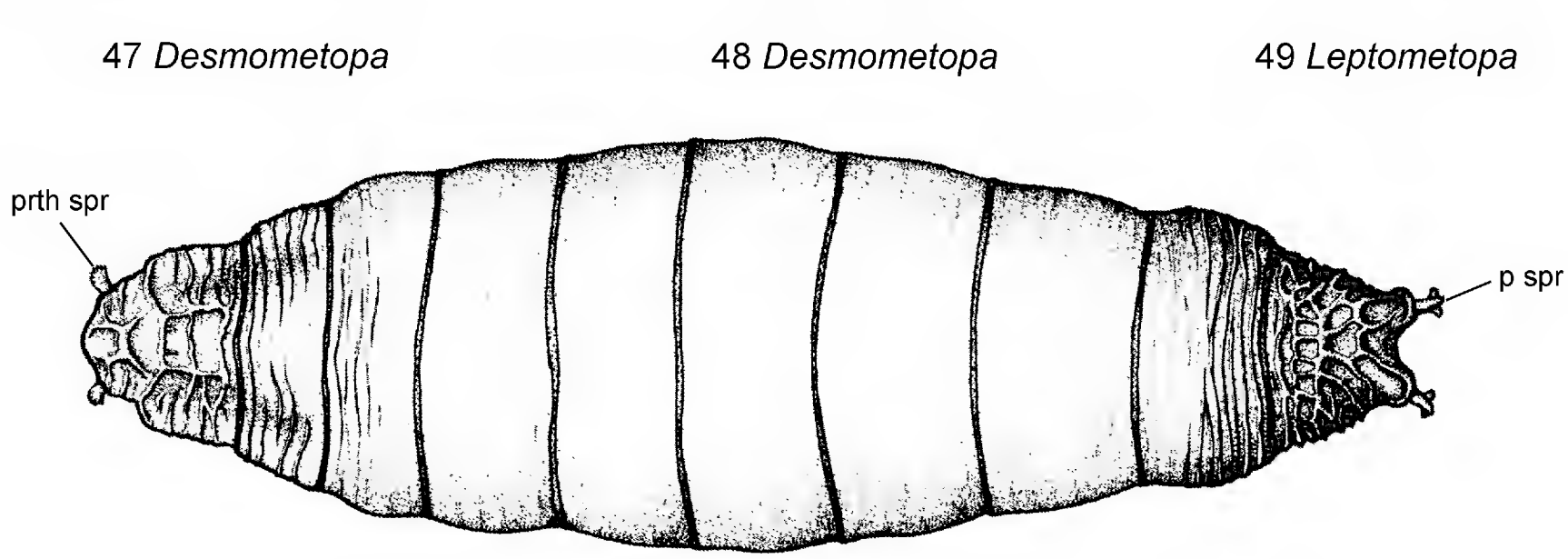
47 *Desmometopa*



48 *Desmometopa*



49 *Leptometopa*



50 *Milichiella*

Figs 95.47–50. Immature stages of Milichiidae: (47) terminal segments of larva of *Desmometopa m-nigrum* (Zetterstedt), posterolateral view; (48) left posterior spiracle of larva of *Desmometopa* sp., caudal view; (49) same, *Leptometopa coquilletti* (Hendel); (50) puparial habitus of *Milichiella tiefii* (Mik), dorsal view (non-Afrotropical). Fig. 47 (Sabrosky 1987*a*, fig. 20); Figs 48, 49 (Hennig 1956, figs 10B, 10A, respectively), Fig. 50 (Roháček 1995, fig. 10).

Abbreviations: p spr – posterior spiracle; prth spr – prothoracic spiracle; pstig tft – peristigmatic tuft; spr op – spiracular opening.

near Ambilobe in northern Madagascar. The genus is distinguished from other madizines by the shortened discal medial cell (*dm*) and the head of the male with highly modified antennae, where the arista is greatly reduced and the postpedicel bears a long, plumose strap-like process (Fig. 34). Deeming (1990) placed this monotypic genus near *Costalima*. Its generic affinities shall be discussed more fully in a future study. Biology and immature stages remain unknown.

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CHLOROPIDAE 96

(Frit Flies, Grass Flies and Eye Gnats)

John W. Ismay, Barbara Ismay and John C. Deeming

Fig. 96.1. Female of *Lagaroceras pulchellum* Lamb (South Africa) (photograph © S.A. Marshall).

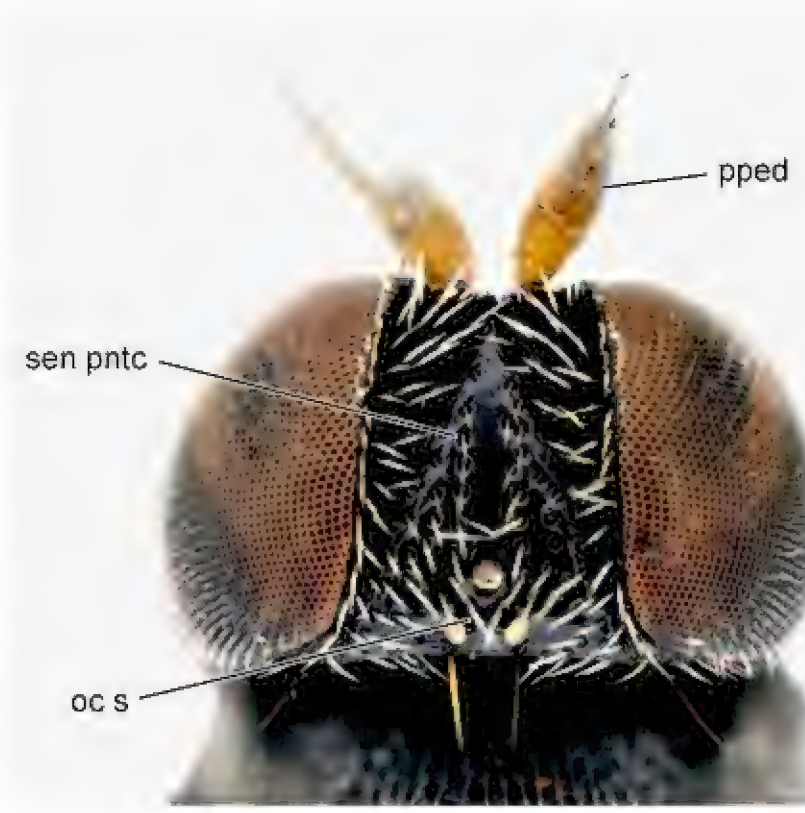
Diagnosis

Small-sized (body length: 0.8–9.5mm) acalyptrate flies (Fig. 1), typically yellow to black or with combinations of two colours, varying from shiny to entirely pruinescent; body shape highly varied, from short and broad (Fig. 62) to greatly elongate (Fig. 103); setae reduced in most genera, but some with nearly all setae found in Acalyptratae, in others virtually all setae absent.

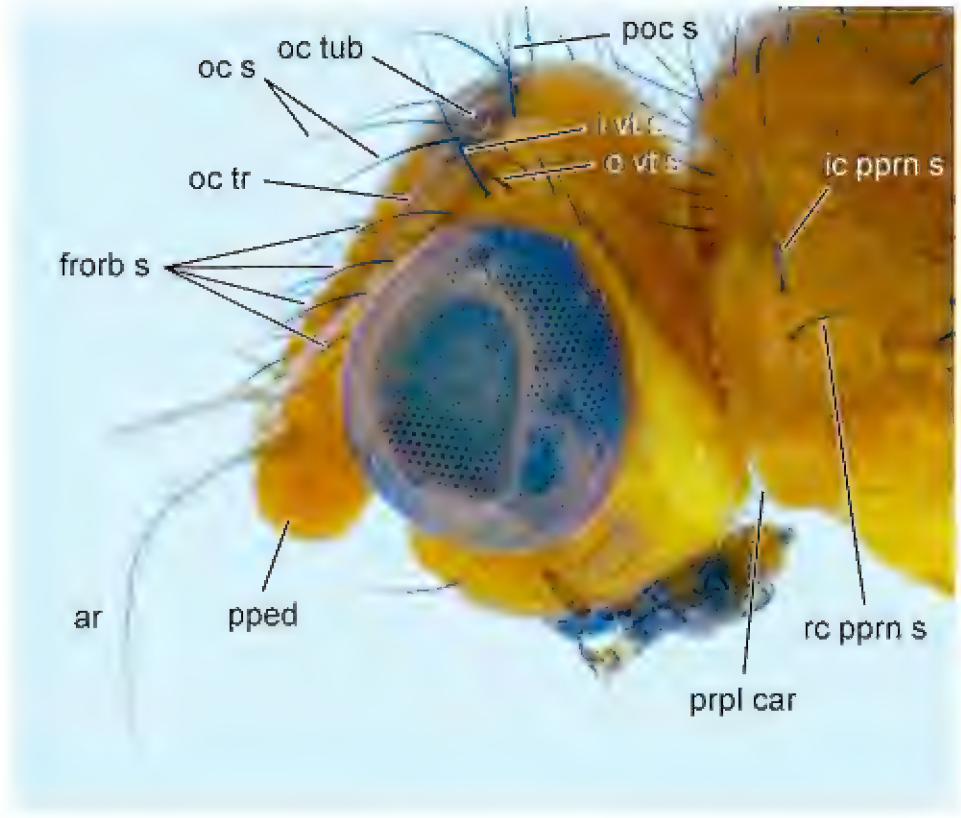
Head usually slightly longer than deep in lateral view, in some species greatly extended beyond anterior margin of eye, or head deeper than long; head wider than thorax in one Afrotropical *Pseudogaurax* Malloch species from Côte d'Ivoire and in genera *Homops* Speiser and *Thressa* Walker; ocellar triangle developed in most species (Figs 16, 19), triangular area on frons extending from ocellar tubercle (Fig. 19) to a varying distance up to anterior margin of frons, usually broader posteriorly and narrowed or pointed anteriorly, or huge, occupying entire frons and broadly rounded anteriorly (*Platycephala* Fallén, *Thressa* and Australian, *Collessimyia* Spencer), varying from yellow to black or patterned, from entirely shiny to pruinescent or patterned, bare or with setulae within lateral margins or setulae more extensive; antenna varying from short, with postpedicel *ca* as long as deep (Fig. 15), to greatly elongate (Fig. 116), or with postpedicel many times longer than deep; scape short and ring-like, slightly longer than deep in *Neoloxotaenia* Sabrosky; pedicel in most genera short, but slightly elongate in some species; anterodorsal corner of postpedicel sometimes extended (Fig. 17); arista varying from bare (Fig. 95) to flattened and greatly thickened (Figs 4, 84) or pectinate with long branches (non-Afrotropical *Thressa*); face flat (Fig. 15) or medially with facial carina (ridge with sharp or flattened anterior margin central to face, either complete (Fig. 14) or incomplete

(Fig. 12)); antennae sunken in antennal foveae (Figs 14, 22) or not (Fig. 15); vibrissal angle varying from not extended before eyes (Fig. 93) to greatly extended, in the latter case gena projecting before antennae, with anterior corner strongly acute (Fig. 15); proboscis short (Fig. 22) or elongate and geniculate (Figs 20, 81), labellum with 3 or many pseudotracheae on each side; compound eye varying from longer than deep (Fig. 95) to deeper than long (Fig. 44), bare (Fig. 10), or clothed in ommatrichia (Fig. 2), margins never closely approximated on frons; fronto-orbital (= frontal setae of Chloropidae workers), ocellar, postocellar, inner and outer vertical setae usually present (Figs 3, 6), but variably developed and oriented; fronto-orbital setae usually small and uniform, but 1 or more setae enlarged, compared to remainder in some genera; ocellar setae proclinate and divergent (Fig. 3) in Siphonellopsinae and Chloropinae, rarely in Oscinellinae, in which these usually erect or reclinate to divergent or cruciate (Figs 2, 8).

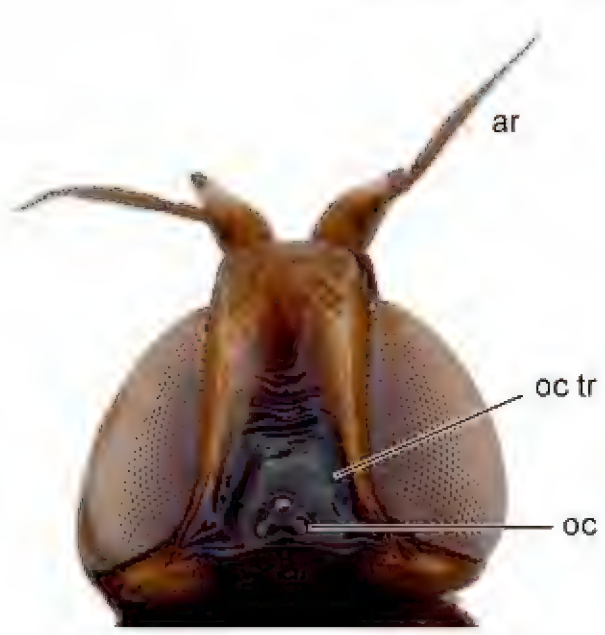
Thorax with propleuron (= proepisternum of Chloropidae workers) always and uniquely within Acalyptratae with distinct, often sharp carina (Fig. 3; see also Marshall *et al*. 2017: 330); scutum usually longer than broad, slightly convex, but highly convex in some genera, almost hemispherical (*Homops*, Fig. 62 and *Siphlus* Loew, Fig. 98), with setulae throughout (Undescribed genus B, Fig. 109), in longitudinal rows (Fig. 117) or absent (*Homops*, Fig. 62), scutum varying from smooth to



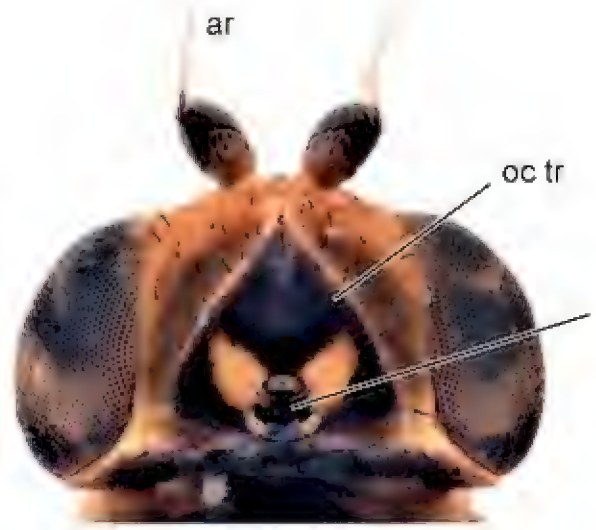
2 *Anomoeoceros*



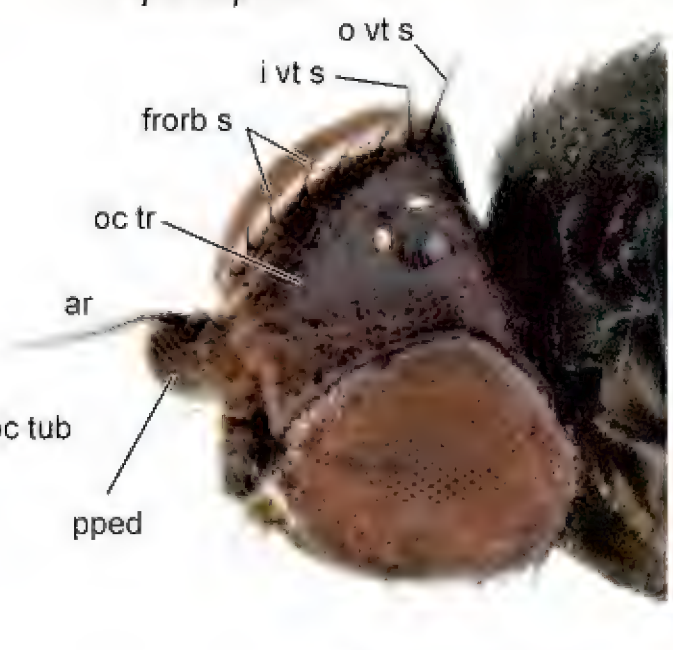
3 *Apotropina*



4 *Camarota*



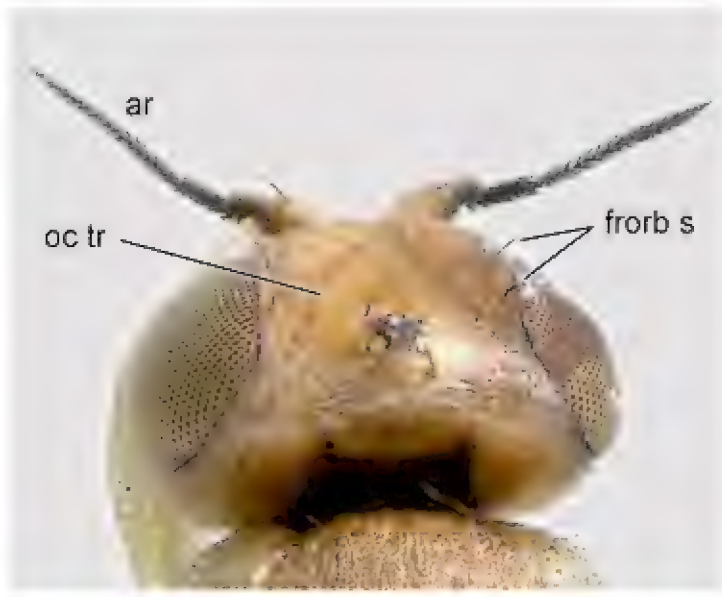
5 *Chlorops*



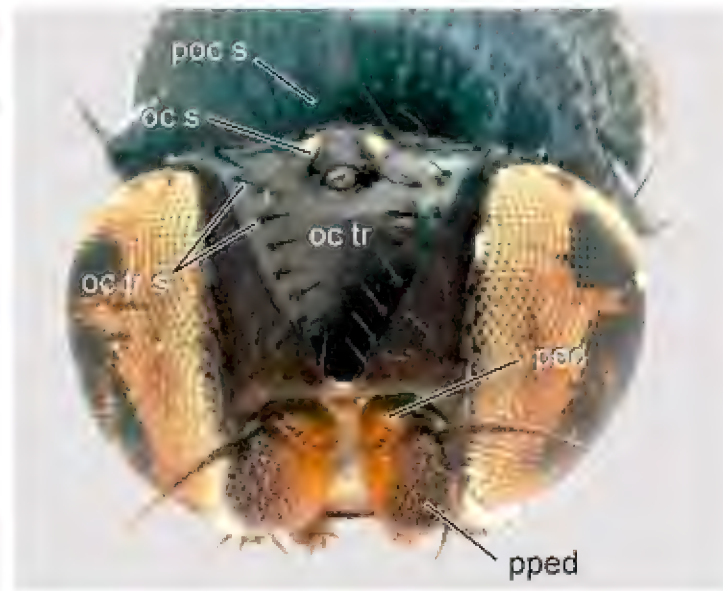
6 *Conioscinella*

Figs 96.2–6. Heads of Chloropidae: (2) *Anomoeoceros punctulatus* (Becker), dorsal view; (3) *Apotropina fuscipleuris* (Becker), lateral view (non-Afrotropical); (4) *Camarota angustifrons* (Bezzi), dorsal view; (5) *Chlorops laevigatus* Becker, dorsal view; (6) *Conioscinella* sp., dorsolateral view (non-Afrotropical).

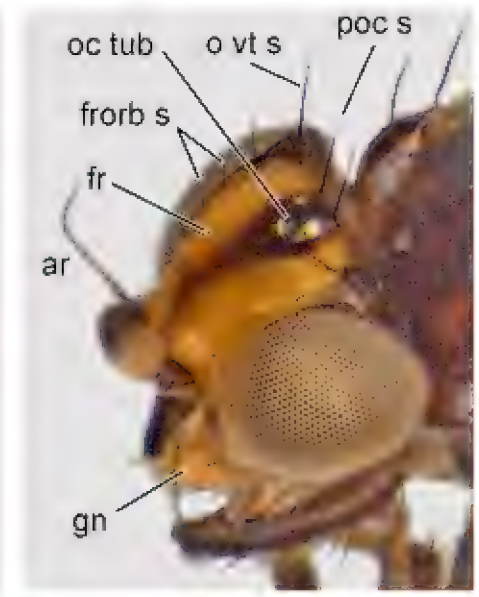
Abbreviations: ar – arista; frorb s – fronto-orbital setae; i vt s – inner vertical seta; ic pprn s – inclinate postpronotal seta; o vt s – outer vertical seta; oc – ocellus; oc s – ocellar seta(e); oc tr – ocellar triangle; oc tub – ocellar tubercle; poc s – postocellar seta; pped – postpedicel; prpl car – propleural carina; rc pprn s – reclinate postpronotal seta; sen pntc – sensory puncture.



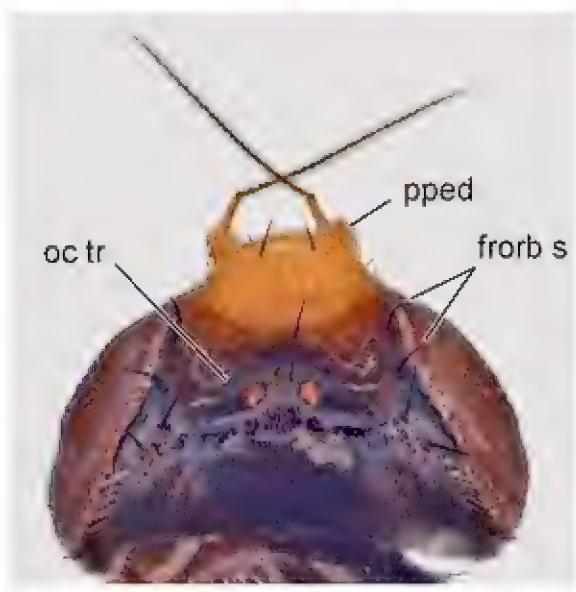
7 *Elachiptera*



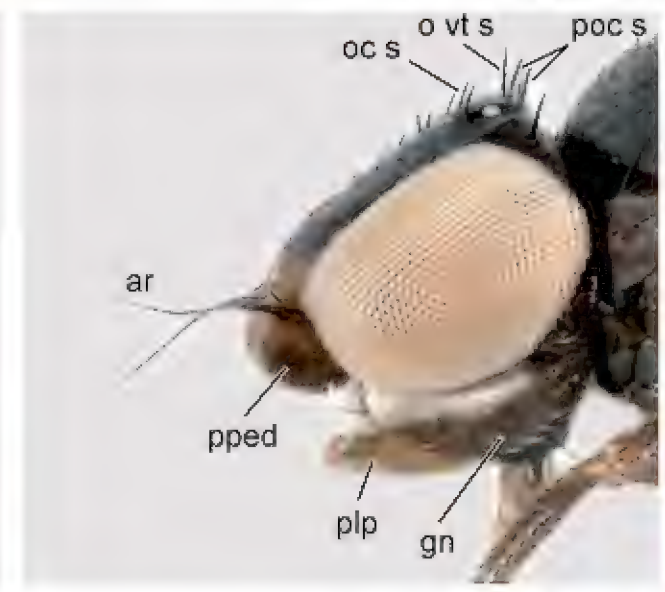
8 *Hapleginella*



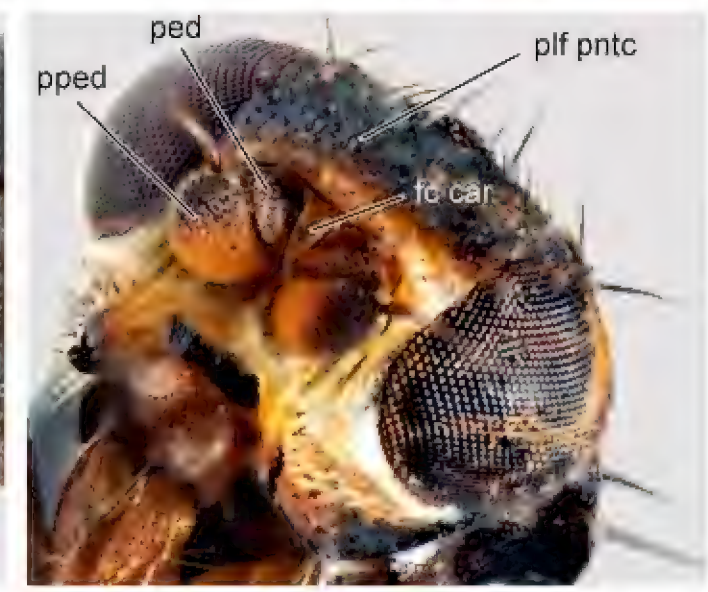
9 *Heteroscinis*



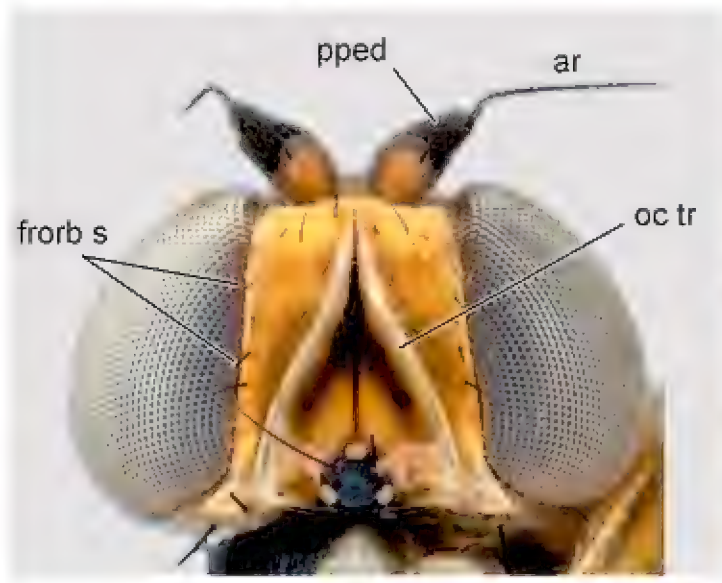
10 *Kwarea*



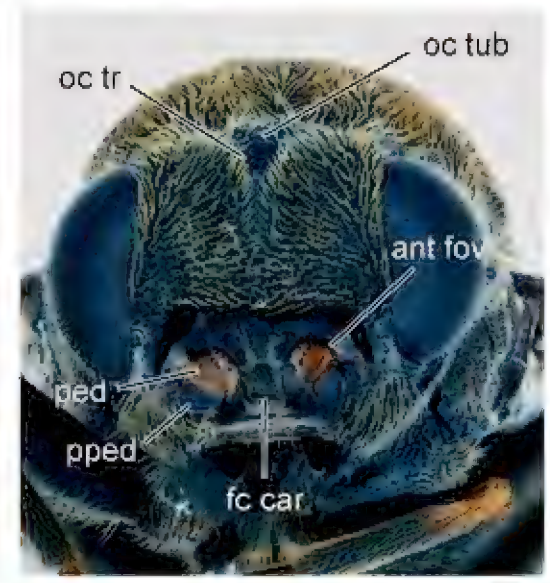
11 *Lasiambia*



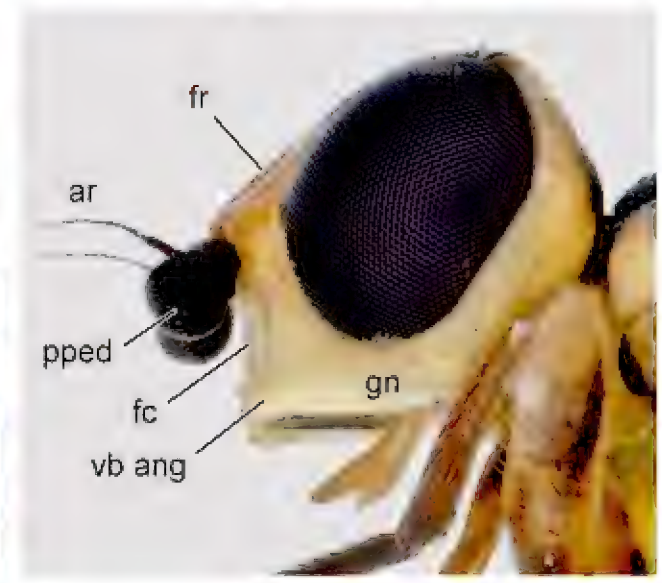
12 *Lasiambia*



13 *Lasiosina*



14 *Lipara*

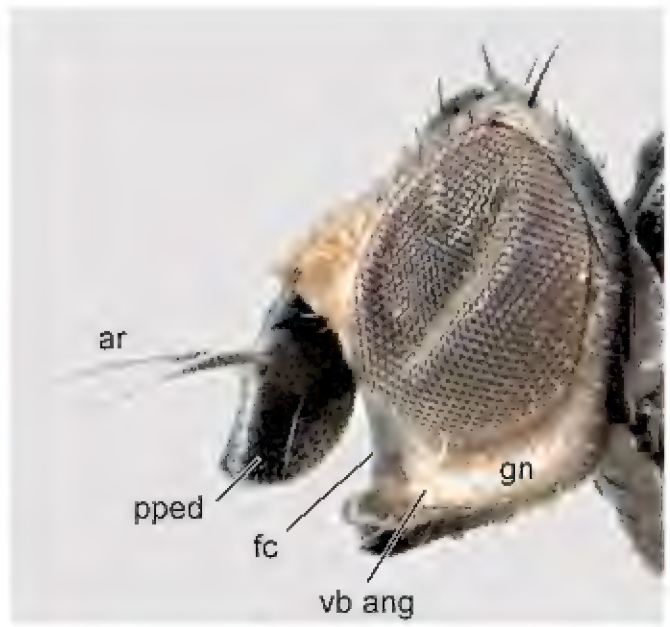


15 *Melanum*

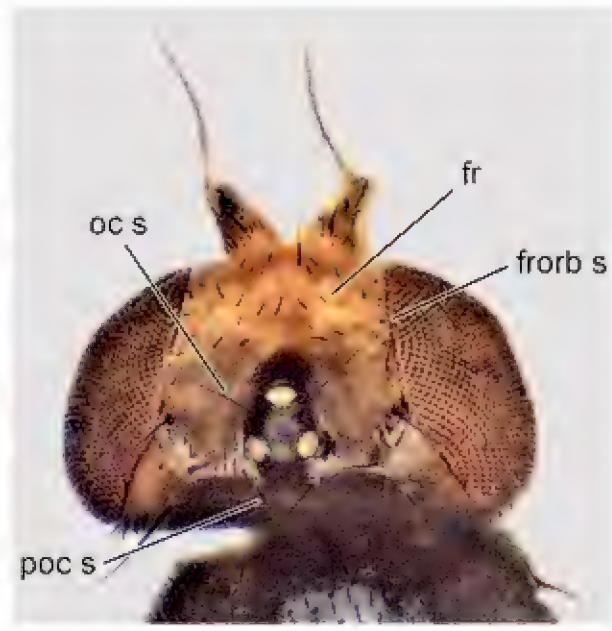
Figs 96.7–15. Heads of Chloropidae: (7) *Elachiptera bimaculata* (Loew), dorsal view; (8) *Hapleginella laevifrons* (Loew), antero-dorsal view (non-Afrotropical); (9) *Heteroscinis hystrix* (Séguy), dorsolateral view; (10) *Kwarea pallidihirta* Sabrosky, dorsal view; (11) *Lasiambia albidipennis* (Strobl), lateral view; (12) *L. palposa* (Fallén), frontal view (non-Afrotropical); (13) *Lasiosina* sp., dorsal view; (14) *Lipara lucens* Meigen, frontal view (non-Afrotropical); (15) *Melanum laterale* (Haliday), lateral view (non-Afrotropical). Figs 7, 11 (© National Museum of Wales).

Abbreviations: ant fov – antennal fovea; ar – arista; fc – face; fc car – facial carina; fr – frons; frorb s – fronto-orbital setae; gn – gena; o vt s – outer vertical seta; oc s – ocellar seta; oc tr – ocellar triangle; oc tr s – ocellar triangle setula; oc tub – ocellar tubercle; ped – pedicel; plf pntc – piliferous puncture; plp – palpus; poc s – postocellar seta; pped – postpedicel; vb ang – vibrissal angle.

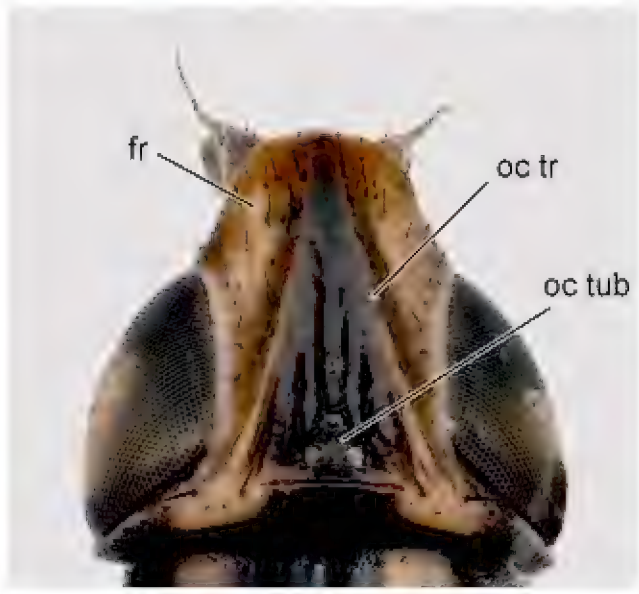
16 *Merochlorops*



17 *Pselaphia*

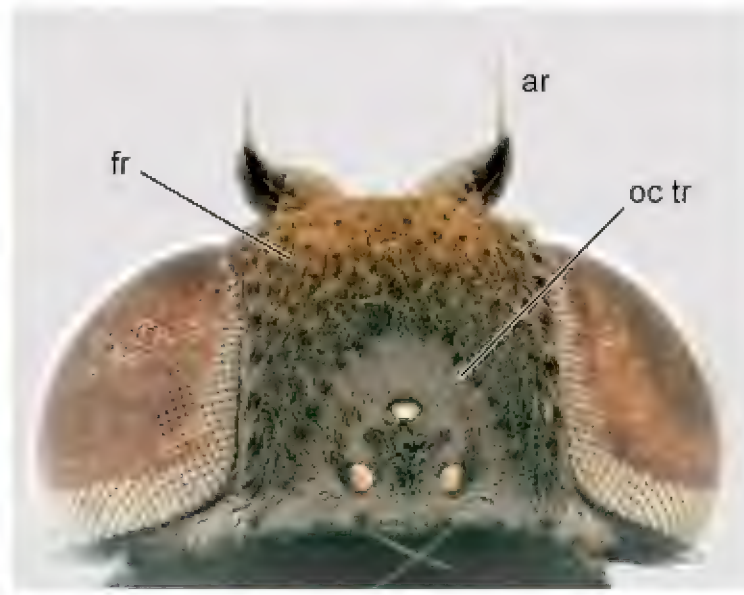


18 *Psilacrum*

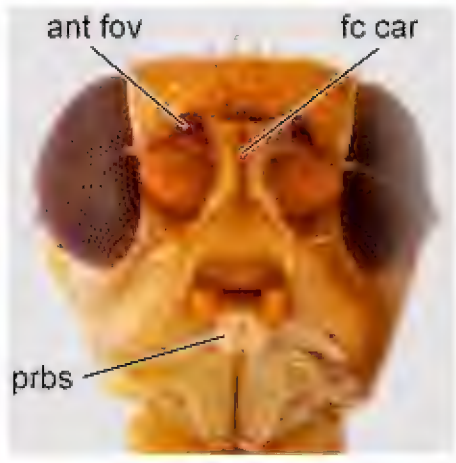


19 *Sabeurina*

20 *Siphonella*

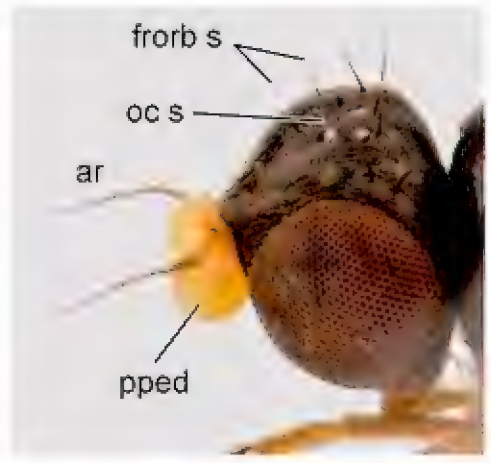


21 *Speccafrons*

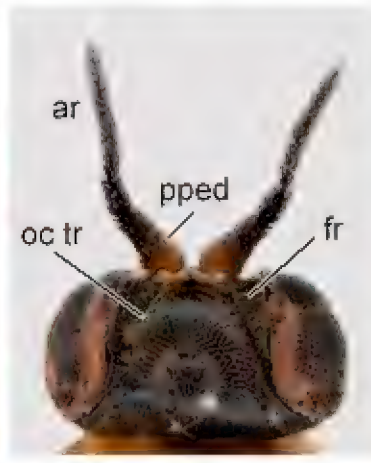


22 *Strobliola*

23 *Trichieurina*



24 Undescribed genus A



25 Undescribed genus C

Figs 96.16–25. Heads of Chloropidae: (16) *Merochlorops vanharteni* Deeming, dorsal view; (17) *Pselaphia cornifera* Becker, lateral view; (18) *Psilacrum* sp., dorsal view; (19) *Sabeurina minuta* (Loew), dorsal view; (20) *Siphonella oscinina* (Fallén), lateral view (non-Afrotropical); (21) *Speccafrons halophila* (Duda), dorsal view (non-Afrotropical); (22) *Strobliola flavofacies* (Becker), frontal view; (23) *Trichieurina pubescens* (Meigen), dorsal view (non-Afrotropical); (24) Undescribed genus A, dorsolateral view; (25) Undescribed genus C, dorsal view. Fig. 17 (© National Museum of Wales), Fig. 20 (© Trustees of Natural History Museum, London).

Abbreviations: ant fov – antennal fovea; ar – arista; fc – face; fc car – facial carina; fr – frons; frorb s – fronto-orbital seta(e); gn – gena; oc s – ocellar seta; oc tr – ocellar triangle; oc tub – ocellar tubercle; poc s – postocellar seta; pped – postpedicel; prbs – proboscis; vb ang – vibrissal angle.

with 3–5 deep long grooves (*Tricimba* Lioy, Fig. 126); setae reduced in most genera, but some Siphonellopsinae with almost all setae found in other Acalyptratae (Fig. 127), to nearly all setae absent (*Homops*, Fig. 62); 1 prescutellar dorsocentral seta usually present (Fig. 96), more in Siphonellopsinae and some Chloropinae and some Oriental Oscinellinae (e.g., *Indonella* Cherian and *Tricimbomyia* Cherian); usually with 1 postpronotal seta (Fig. 128), but 2 in Siphonellopsinae, 1 directed over scutum (inclinate), the other posteriorly (reclinate) (Fig. 3), Siphonellopsinae with 1 or 2 upright scapular setae medial to postpronotum, additional setae in some Oscinellinae; notopleural setae (Figs 127, 128) varying from absent to 1 + 1 or 1 + 2 setae or more in some genera; in Afrotropical Oscinellinae no supra-alar seta present; 2 or more pairs of setae present on margins of scutellum (Fig. 133); katepisternum rarely with dorsal seta present (*Cadrema* Walker, Fig. 130), upper $^1/_2$ of pleura usually shiny, but pruinescent in some genera (*Aphanotrigonum* Duda, Fig. 31), bare or anepisternum with setulae in some genera (*Rhodesiella* Adams, Fig. 129), lower pleura pruinescent in many species. Wings usually present, but reduced or absent (*Alombus* Becker (Fig. 27), *Anatrichus* Loew (those species formerly in *Myrmecosepsis* Becker) (Fig. 76), some *Conioscinella* Duda and *Elachiptera* Macquart), some with wing markings (e.g., *Apotropina* Hendel, *Chromatopterum* Becker (Fig. 47), *Gampsocera* Schiner (Fig. 57), *Pseudochromatopterum* Deeming (Fig. 121) and *Rhodesiella*); venation relatively uniform (Figs 148, 153), reduced, but with great variation in detail; wing short and broad in some genera (e.g., *Rhodesiella*, Fig. 152), elongate in others (e.g., *Stenoscinis* Malloch, Fig. 103); costal vein (*C*) with subcostal break, but without humeral break (Figs 145, 148, 153); subcostal vein (*Sc*) reduced in apical $^1/_2$ (Figs 148, 153); costal ratios (*i.e.*, distance from basicosta to end of R_1 (first sector); R_1 to R_{2+3} (second sector); R_{2+3} to R_{4+5} (third sector) and R_{4+5} to M_1 (fourth sector)), with second costal sector longer (*Psilacrum* Becker, Fig. 151) or shorter in some genera (some *Siphunculina* Rondani, Fig. 124); crossvein *dm–m* absent in a few species (Fig. 53); costal vein (*C*) extending to vein M_1 (Fig. 148) in all Oscinellinae, except in a few species (e.g., *Calamoncosis* Enderlein, Figs 39, 141, *Dicraeus* Loew, Fig. 50 and *Scoliophthalmus* Becker, Fig. 95), in which it ends between veins R_{4+5} and M_1 (Fig. 141); vein M_4 frequently with slight flexure or kink at or basal to middle of cell *bm+dm* (Figs 148, 153), a groundplan of all extant and fossil Chloropidae; veins A_1, *CuA+CuP* and cell *cua* absent; crossvein *bm–m* absent; cell *cua* already absent in Eocene fossil Chloropidae (Tschirnhaus & Hoffeins 2009) and kink in vein M_4 of discal medial cell (*dm*) marks point where crossvein *bm–m* existed; anal lobe variable. Legs usually slender, without developed setae, except at anteroventral corner of mid tibia; spur or seta present at anteroventral corner of hind tibia in some genera (e.g., *Apotropina* and *Cadrema*, Fig. 156); tibial organ present or absent in both sexes (Fig. 159), a clearly defined area densely clothed in microtrichia on dorsal surface of hind tibia in some genera; mid femoral organ (Fig. 160) often present in male, composed of group of stud-like, short, robust setulae on dorsal surface in some Oscinellinae and in *Cryptonevra* Lioy (Chloropinae) (Ismay 1975), femoral organ in *Rhodesiella plumiger* (Meigen, 1830) present on both mid and hind femora of males (Andersson 1977) and in females of some species of *Rhodesiella* and *Scoliophthalmus* (Nartshuk 1987: 43, figs 1–6); fore femur rarely enlarged (*Epimadiza* Becker); hind femur greatly thickened in some genera (in the Afrotropics in *Meromyza* Meigen, *Meromyzella* Andersson, *Pachylophus* Loew, *Platycephala* and *pro parte* in *Rhodesiella* Adams) and tibia correspondingly curved to fit (Fig. 158).

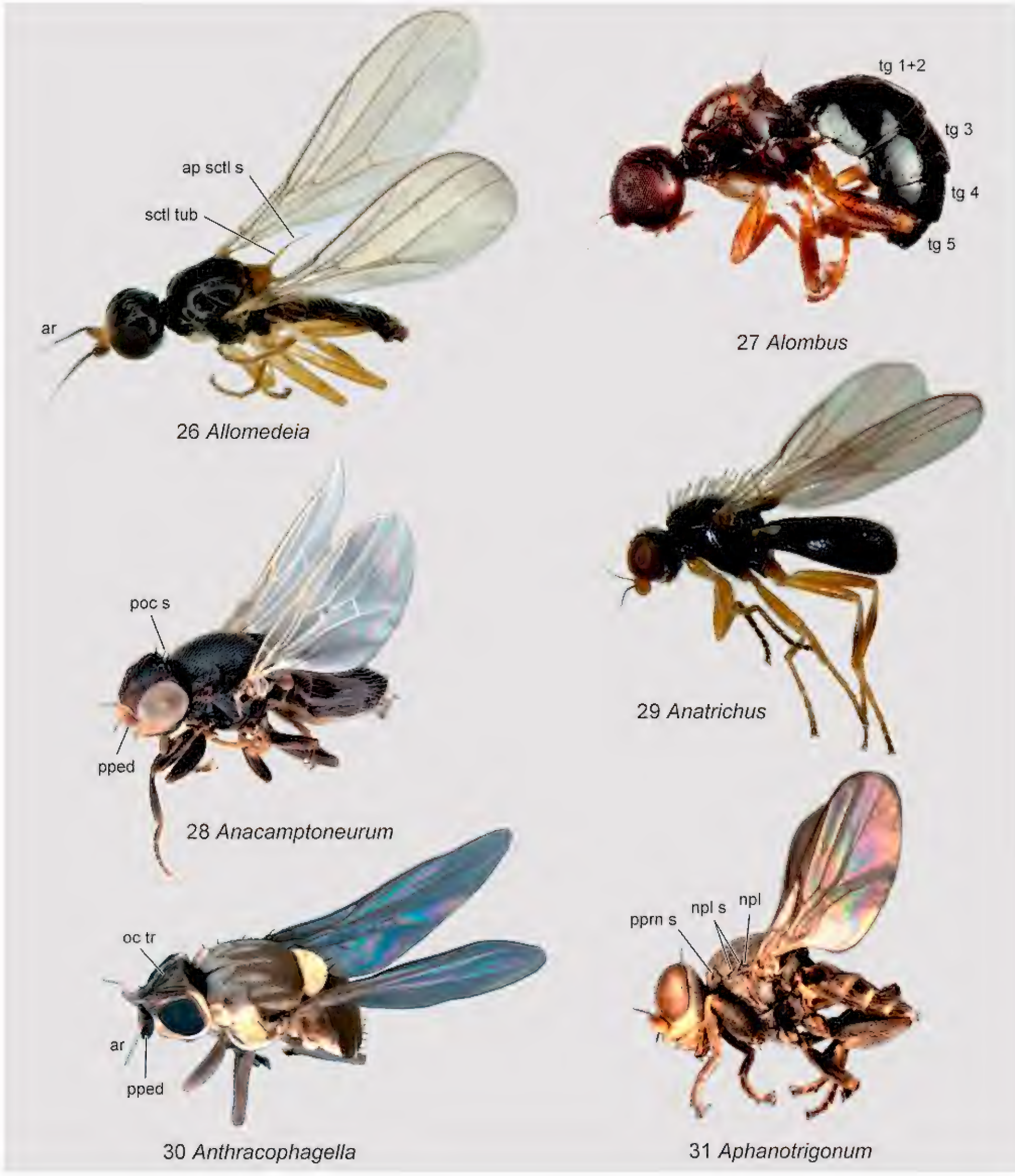
The following account of the terminalia follows Riccardi & Amorim (2020). Abdomen usually with 5 male pregenital tergites, or reduced to 4 (*Chromatopterum*, Fig. 47); male postabdomen reduced (compared to related families), with externally visible tergite 6 absent, in *Anatrichus* inclusive of the former genus *Togeciphus* Nishijima (non-Afrotropical) tergites reduced further; pregenital sclerites symmetrical in Chloropinae and Oscinellinae, but asymmetrical in Siphonellopsinae (Fig. 172); surstylus free and articulated in Siphonellopsinae (Figs 163, 164, 172) and variable and articulated in some Oscinellinae (Figs 168, 170), but reduced and either flat against, or articulated with epandrium in some Chloropinae (e.g., *Lasiosina* Becker) (Figs 161, 162, 166); cercus usually present, fused or separate, greatly varying within and between genera, reduced to mesolobus (between insertion of surstyli) in Chloropinae; postgonite usually with setulae and pores; pregonite bare, usually lateral or dorsal to postgonite; phallus composed of sclerotised basiphallus variable in shape, followed by distiphallus (Figs 161, 162), short and membranous in most genera, but longer in some *Cryptonevra*; hypandrium highly variable in Chloropinae (Fig. 167), Oscinellinae (Figs 169, 171) and Siphonellopsinae (Fig. 165); males of a few genera with 1 or 2 lateral pairs of eversible vesicles each side before epandrium (some *Chlorops* Meigen, some *Chloropsina* Becker, *Cryptonevra*, *Neoloxotaenia* Sabrosky, *Polyodaspis* Duda and *Thaumatomyia* Zenker); female postabdomen (Figs 174, 175) simple, in most species with weakly sclerotised structure, but in some species tip heavily sclerotised and parts fused, compressed into blade-like structure (e.g., some *Diplotoxa* (*Pseudopachychaeta* Strobl) and *Calamoncosis*, Fig. 173), or cercus with numerous stiffened setulae (*Arcuator* Sabrosky); 2 spermathecae present, but not sclerotised.

Adult Chloropidae may be confused with Milichiidae (see Chapter 95), but the latter family has inclinate fronto-orbital setae, a character not found in Chloropidae, although a few genera have somewhat larger setulae present on the frons and care must be taken not to confuse these with fronto-orbital setae. Chloropidae may also be superficially confused with Asteiidae (see Chapter 92), but these lack the propleural carina. All other families of Acalyptratae also lack the propleural carina. The presence of an ocellar triangle is not an infallible guide to a fly belonging to the Chloropidae, as there are numerous species in which it is dull and pruinescent and also species in other families may possess a shiny triangle in the same position. The Afrotropical fauna includes a number of species with reduced wings, but they can be recognised by the presence of the propleural carina.

Biology and immature stages

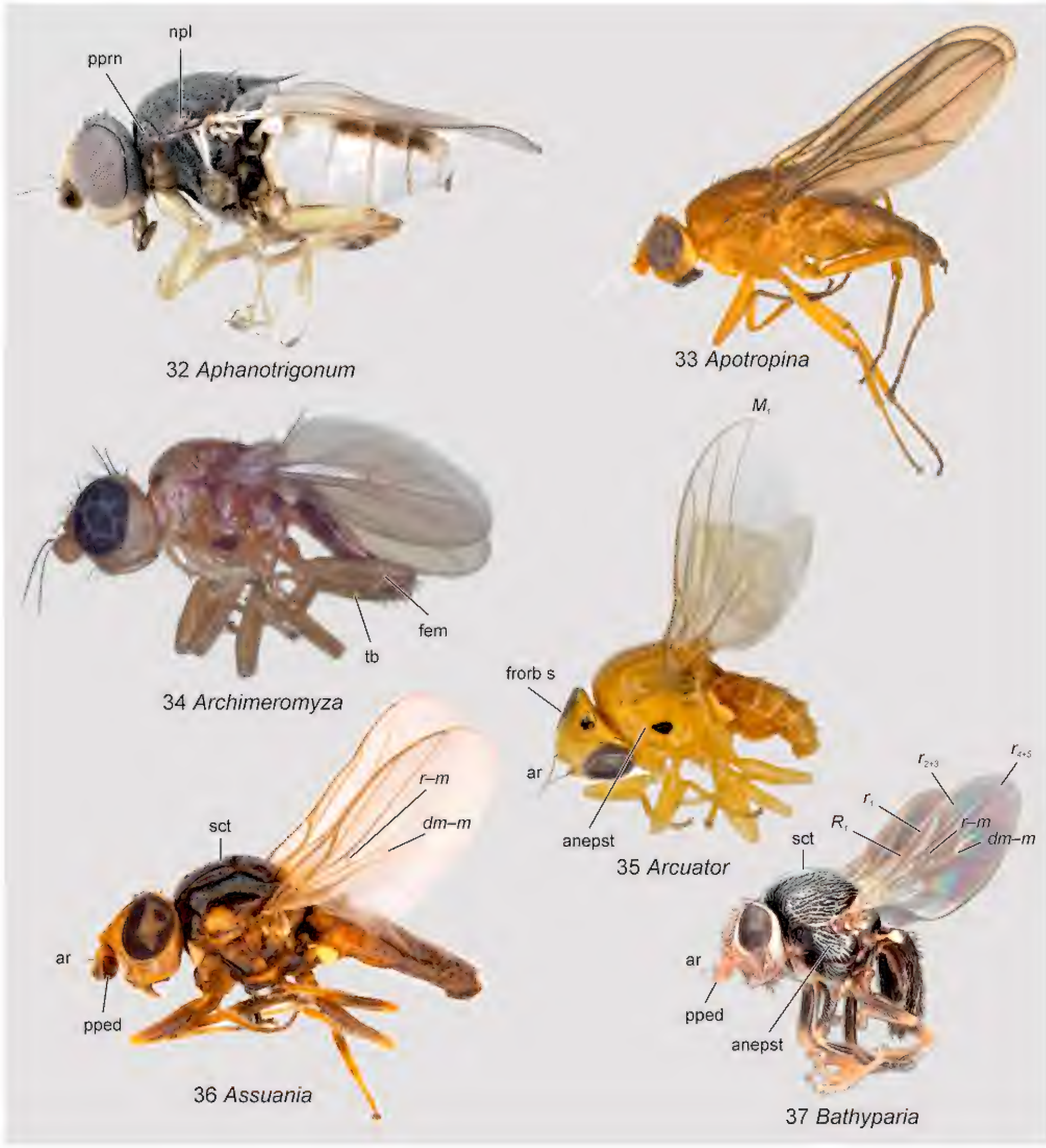
The fauna of Chloropidae is both diverse and abundant in the Afrotropics and is one of the dominant families of Diptera in many habitat types, especially grassland and savanna habitats, grading into wetlands.

Adult biology in the family is also diverse. *Eutropha* Loew and non-Afrotropical *Pemphigonotus* Lamb adults occur on or near the seashore and feed on stranded fish and jellyfish. *Eutropha*



Figs 96.26–31. Habitus of Chloropidae (lateral views): (26) *Allomedeia* sp.; (27) *Alombus* sp.; (28) *Anacamptoneurum obliquum* Becker; (29) *Anatrichus erinaceus* Loew; (30) *Anthracophagella albovariegata* (Thomson) (non-Afrotropical); (31) *Aphanotrigonum femorellum* Collin (non-Afrotropical). Fig. 27 (© Trustees of Natural History Museum, London).

Abbreviations: ap sctl s – apical scutellar seta; ar – arista; npl – notopleuron; npl s – notopleural setae; oc tr – ocellar triangle; poc s – postocellar seta; pped – postpedicel; pprn s – postpronotal seta; sctl tub – scutellar tubercle; tg – tergite.



Figs 96.32–37. Habitus of Chloropidae (lateral views): (32) *Aphanotrigonum subfasciellum* Collin; (33) *Apotropina fuscipleuris* (Becker) (non-Afrotropical); (34) *Archimeromyza humeralis* Deeming; (35) *Arcuator munroi* Sabrosky; (36) *Assuania thalhammeri* (Strobl) (non-Afrotropical); (37) *Bathyparia praeclara* (Lamb). Fig. 32 (© National Museum of Wales), Fig. 34 (© Trustees of Natural History Museum, London), Fig. 37 (courtesy Y. Ang).

Abbreviations: anepst – anepisternum; ar – arista; *dm–m* – discal medial crossvein; fem – femur; frorb s – fronto-orbital seta; M_1 – first branch of media; npl – notopleuron; pped – postpedicel; pprn – postpronotum; R_1 – anterior branch of radius; r_1 – first radial cell; r_{2+3} – second + third radial cell; r_{4+5} – fourth + fifth radial cells; *r–m* – radial–medial crossvein; sct – scutum; tb – tibia.

lindneri Sabrosky, 1972, has even been reared from dead Cape fur seal, *Arctocephalus pusillus* (Schreber) (Otariidae), carcasses in Southern Africa (Kirk-Spriggs 2007). In the Afrotropics, *Anomoeoceros* Lamb females are attracted to spiders in their webs, presumably attracted to gore from the spiders' prey (Ismay 1979) and females of *Pseudogaurax taiensis* Deeming, 1989 and *P. brevifacialis* Deeming, 1989 have been observed alighting on the spider *Nephila turneri* Blackwall (Araneidae) in their webs in Côte d'Ivoire (Boulard *et al*. 1989). Species of *Mimosepsis* Sabrosky resemble ants (Fig. 75) and coexist with them (Deeming 1976). Chloropidae are also known as kleptoparasites of other species, the adult flies being attracted to and feeding upon the exudates of other insects damaged by predators, such as spiders (Marshall 2012: 371; Marshall & Kirk-Spriggs 2017: 148, fig. 4.15), a habit recorded for the genera *Anomoeoceros*, *Conioscinella*, *Gaurax* Loew and *Olcella* Enderlein (non-Afrotropical). *Trachysiphonella pori* Harkness & Ismay, 1975, was observed participating in the ant-meal of a spider (Harkness & Ismay 1975). Some species are attracted as adults to young shoots of plants, but do not cause damage, a habit also recorded for the genera *Arcuator* (Sabrosky 1985) and *Notaulacella* Enderlein (J.W. Ismay, unpubl.) in the Australasian Region. *Apotropina* is known to form very large aggregations of adult flies in caves and similar situations (M. von Tschirnhaus, pers. comm. 2021). In the Palaearctic Region, *Thaumatomyia notata* (Meigen, 1830) is noted for forming aggregations in buildings in winter and can render houses uninhabitable (Kotrba & Nartshuk 2009; Nartshuk 2000*b*; M. von Tschirnhaus, pers. comm. 2021). Kotrba (2009) studied the vesicles of *T. notata* and found strong evidence that these could be for dispersing pheromones from the glands surrounding them in the body and suggested that the use of this pheromone should be investigated as a potential control mechanism. The larvae of *T. notata* are predaceous on aphids, including the Sugar beet root aphid, *Pemphigus betae* Doane (Aphididae) (Nartshuk 2014) and Chloropidae in general are attracted to high concentrations of honeydew-producing Hemiptera: Sternorrhyncha, such as aphids on reeds and on tree leaves (J.W. Ismay, unpubl.).

The life histories of Chloropidae are more varied than in most other families of Diptera, with the exception of the Phoridae (see Chapter 59) (Ferrar 1987: 274). Amongst the plant-associated species there are two large groups of life histories, one with larvae developing on growing plants, especially grasses (Poaceae), and the other as scavengers, feeding on micro-organisms in damaged parts in growing plants. They are also predators, parasites and parasitoids of other invertebrates and frogs (the last-mentioned non-Afrotropical) and they have been reared from various dead mammals, birds, reptiles, frogs and many invertebrates and from mammal dung and bird guano (Kanmyia 1983), bat guano (A.H. Kirk-Spriggs, pers. comm. 2020) and fungi. Some are vectors of diseases of mammals and humans and many cause damage to crops, including: millets, Oats (*Avena sativa* L.), rice (*Oryza* spp.), Sorghum, *Sorghum bicolor* (L.) Moench, Tef, *Eragrostis tef* (Zucc.) Trotter and Wheat, *Triticum aestivum* L. (all Poaceae) (see "Economic significance" below) and some are important pollinators, feeding on pollen and nectar (Proctor *et al*. 2012).

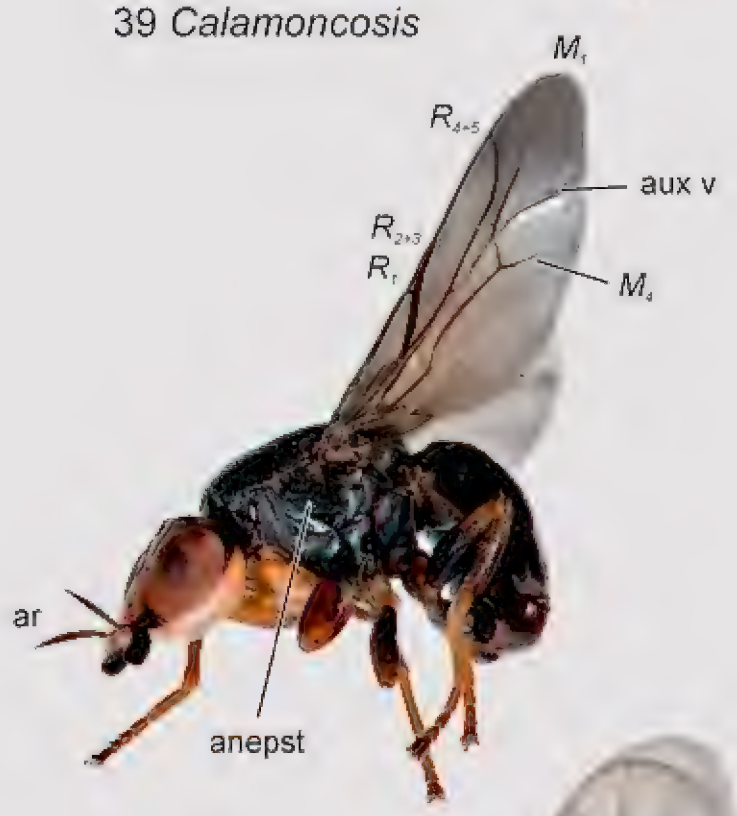
An account of chloropid eggs was published by Gaponov (2000). The egg is cylindrical with surface sculpture and ovoviviparity is known in a few species (Deeming 2018; Pollock 1996; Spencer 1985). The eggs are elongate and cylindrical, tapering at both ends and slightly curved and in some cases the egg is greatly elongate (10 × as long as wide) (Deeming & Al-Dhafer 2012). Colour varies from white to yellow to blackish (in *Lipara* Meigen). The surface of the chorion is often strongly sculptured and varies from genus to genus, but in gall-forming species, such as *Lipara,* the chorion is very weakly sculptured. Deeming & Al-Dhafer (2012) described the egg of *Scolioph-thalmus cryptonevriformis* Deeming & Al-Dhafer, 2012, while Nartshuk & Andersson (2013: 23) provided an excellent overview, including illustrations of the eggs of northern Palaearctic genera. Ferrar (1987: 613) illustrated a range of chloropid eggs and Grochowska (2002, 2007*b*, 2008*a*, *b*, *c*, 2013) described and illustrated various non-Afrotropical eggs as detailed below. The larva (Fig. 176) is of the usual schizophoran type, generally featureless, but with creeping welts limited to the ventral surface (the size and arrangement of spicules is diagnostic). The pseudocephalon and prothorax express numerous external diagnostic features (Figs 177, 180), useful in generic and species-level recognition (Nye 1958), including the maxillary palpus, antenna, arrangement of cirri (Fig. 177) and the number and arrangement of spiracular papillae on the prothoracic spiracle (Fig. 178). The internal cephaloskeleton (Fig. 180) is useful in differentiating species and the posterior spiracles (Figs 176, 179) are also diagnostic, especially the shape and size of the spiracular opening and peristigmatic tufts (Fig. 179). The non-ovoviviparous species of Chloropidae have three larval stages.

The puparium (Figs 181, 182) has corresponding larval features, either in the main part or in the cap and these are diagnostic in the same way as the larval features. It is thicker and shorter than the last larval stage and varies in colour. Puparia have some surface sculpture that varies from rather smooth to highly wrinkled, but are dorsoventrally flattened anteriorly. Descriptions of immature stages of some Afrotropical species are available: Deeming 1974, 1977 (*Pachylophus*); 1979 (*Dicraeus*); 1981a (Chloropinae); 2003 (*Oscinella* Becker); 2018 (*Pachylophus*); Deeming & Al-Dhafer 2012 (Arabian Peninsula species). In *Pachylophus beckeri* Curran, 1928, the maturing larva pupariates and the prothoracic spiracles migrate to the ventral surface of the puparium and pierce the aerenchyma of the host-plant (Deeming 1974), while *Strobliola flavofacies* (Becker, 1910) has the posterior spiracles of the puparium developed into two curved diverging blades (Deeming & Al-Dhafer 2012). The third-instar larva and puparium of *Eutropha lindneri* were described by Kirk-Spriggs (2007) from Namibia. Grochowska provided detailed descriptions of all immature stages of the non-Afrotropical species *Calamoncosis aprica* (Meigen, 1830) (Grochowska 2002), *Cryptonevra diadema* (Meigen, 1830) (Grochowska 2008*b*), *C. flavitarsis* (Meigen, 1830) (Grochowska 2008*c*), *C. nigritarsis* (Duda, 1933) (Grochowska 2007*b*), *Lipara lucens* Meigen 1830 (Grochowska 2013) and *Microcercis zuercheri* (Duda, 1933) (Grochowska 2008*a*).

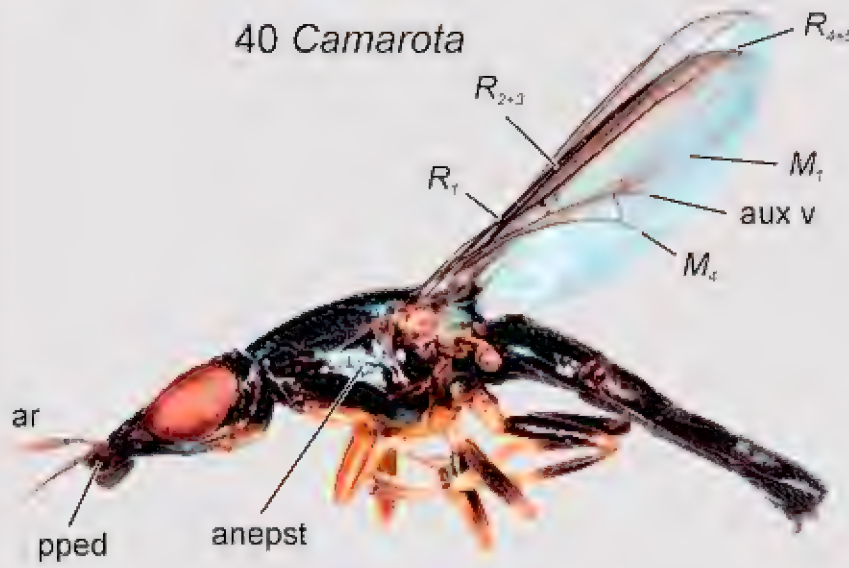
Larvae of the Palaearctic species, *Aphanotrigonum trilineatum* (Meigen, 1830) are saprophagous in various cereals and grasses (Ferrar 1987: 110; Wendt 1968). Some larval structures were illustrated by Kreiter (1928) and Nartshuk (1987). *Cadrema* has been reared from decaying plant tissue and decaying animals, including Mollusca, pig dung, cotton bolls and

38 *Cadrema*

39 *Calamoncosis*



40 *Camarota*



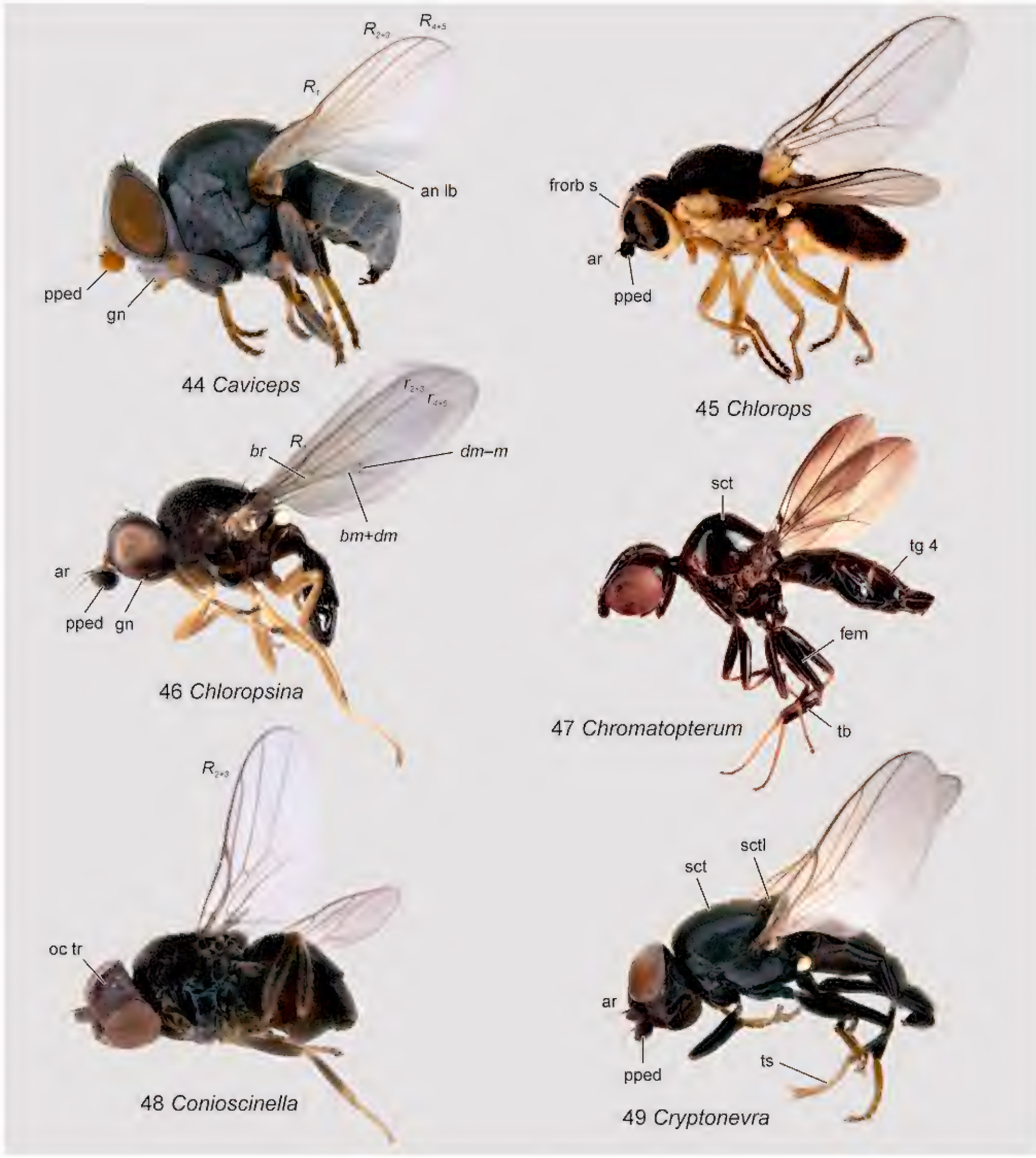
41 *Camarota*

42 *Camarota*

43 *Camptoscinella*

Figs 96.38–43. Habitus of Chloropidae (lateral views): (38) *Cadrema pallida* (Loew); (39) *Calamoncosis abbreviata* Deeming (non-Afrotropical); (40) *Camarota angustifrons* Bezzi; (41) *Cam. curvipennis* (Latreille); (42) *Cam. cylindrica* Deeming; (43) *Camptoscinella annulitibia* Sabrosky. Figs 39, 42 (© National Museum of Wales), Fig. 41 (courtesy Y. Ang), Fig. 43 (© Trustees of Natural History Museum, London).

Abbreviations: anepst – anepisternum; ar – arista; aux v – auxiliary vein; M_1 – first branch of media; M_4 – fourth branch of media; pped – postpedicel; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius.



Figs 96.44–49. Habitus of Chloropidae (lateral views): (44) *Caviceps* sp. (non-Afrotropical); (45) *Chlorops laevigatus* Becker; (46) *Chloropsina* sp.; (47) *Chromatopterum linguatum* Séguy; (48) *Conioscinella* sp. (non-Afrotropical); (49) *Cryptonevra flavitarsis* (Meigen) (non-Afrotropical). Fig. 47 (© Trustees of Natural History Museum, London).

Abbreviations: an lb – anal lobe; ar – arista; *bm+dm* – basal medial cell + discal medial cell; *br* – basal radial cell; *dm–m* – discal medial crossvein; fem – femur; frorb s – fronto-orbital seta; gn – gena; oc tr – ocellar triangle; pped – postpedicel; R_1 – anterior branch of radius; r_{2+3} – second + third radial cell; R_{2+3} – second branch of radius; r_{4+5} – fourth + fifth radial cells; R_{4+5} – third branch of radius; sct – scutum; sctl – scutellum; tb – tibia; tg – tergite; ts – tarsus.

decaying marine animals (Bezzi 1928: 150; Ferrar 1987: 110; Nartshuk 2010a). Nartshuk (2010a) recorded *C. minor* (de Meijere, 1908) as being reared from *Capsicum* (Solanaceae) in Malaysia and from rotting coconuts in Seychelles. *Cadrema pallida* (Loew, 1866) has also been reared from honeydew on leaves of *Ficus* (Moraceae) in Seychelles (J.C. Deeming, unpubl.) and the puparium was described by Bohart & Gressitt (1951). *Calamoncosis* has been reared from plant tissue of *Glyceria* and *Phragmites* (both Poaceae) in the Palaearctic and as an inquiline from plant tissue of *Phragmites* damaged by other insects (Collin 1946; Ferrar 1987: 110). Deeming & Al-Dhafer (2012) commented that *Calamoncosis* species attack Sorghum under water-stress in the Afrotropical Region.

Larvae of *Chlorops* Meigen are primary stem-borers of grasses and sedges and *C. pumilionis* (Bjerkander, 1778), the Gout fly, is a serious pest of cultivated cereals, including Barley, *Hordeum vulgare* L. and Wheat outside of the region (Nartshuk & Andersson 2013: 179), while some other species are recorded as minor pests (Ferrar 1987: 115). There is a total of 476 papers and dissertations published dealing only with this pest species (M. von Tschirnhaus, pers. comm. 2021). The larvae and/or the puparia of five Palaearctic species of *Chlorops* are discussed by Balachowsky & Mesnil (1935: 935). The immature stages of *Chloropsina* have been found in *Citrus* roots in Hawaii (Ferrar 1987: 115) and shoots of the grass *Paspalum vaginatum* Swartz (Poaceae) in Nigeria, the puparium was partially described from the latter locality by Deeming (1981a), who described the puparium and cephaloskeleton of *C. litoralis* Deeming, 1981. Species of *Conioscinella* have been reared from decaying plant material, spider egg masses, grass stems and cereals (Ferrar 1987: 110). Nye (1958) described the immature stages of *C. frontella* (Fallén, 1820) and *C. mimula* Collin, 1946.

Larvae of *Dicraeus* occur in the flower heads of grasses and destroy the developing seeds at the milky grain stage (Ferrar 1987: 111) and are regarded as minor pest species. In West Africa, Deeming (1979) recorded *D. pennisetivora* Deeming, 1979 feeding on the millet *Pennisetum glaucum* (L.) R. Br. causing extensive damage. Extralimital species of *Diplotoxa* Loew *sensu stricto* have been reared from the seed heads of sedges, several *Eleocharis* (Cyperaceae) and larvae have been discovered (Ferrar 1987: 115; Valley *et al*. 1969). The Nearctic species *D.* (*Elliponeura*) *debilis* (Loew, 1869) is also known to be a primary invader of inflorescences of *Eleocharis* (Ferrar 1987: 115; Valley *et al*. 1969). The immature stages of extralimital species of *Diplotoxa* (*Pseudopachychaeta*) are further known to develop in seed heads of Cyperaceae and are phytophagous (Nartshuk & Andersson 2013: 222) and Nartshuk (1987) illustrated the puparium (p. 91) and cephaloskeleton (p. 99) of the Palaearctic *D.* (*P.*) *ruficeps* (Zetterstedt, 1838). The writers have further reared the same species from the seed heads of *Eriophorum* (Cyperaceae) species.

Extralimital species of *Elachiptera* are well-known as invaders of plant tissue damaged by other organisms (Ferrar 1987: 111; Tschirnhaus 2017) and *E. occipitalis* Becker, 1910 has been reared from Sorghum shoots in the Afrotropics (J.C. Deeming, unpubl.). Ferrar (1987: 618, 619) included figures of the cephaloskeleton and the prothoracic spiracle of an *Elachiptera* species. Immature stages (Figs 176, 178–181) were described by Sabrosky (1987: 1063).

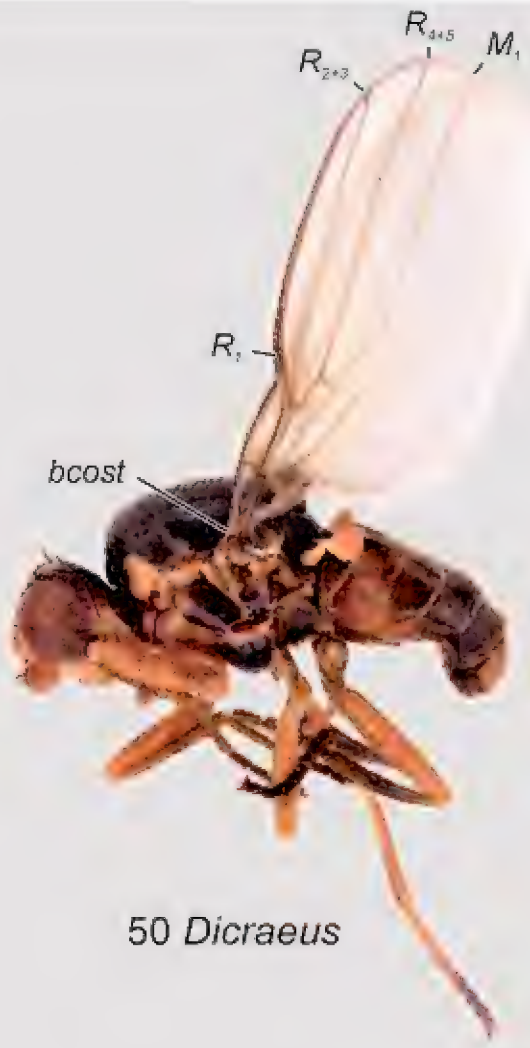
The immature stages of *Elachiptereicus abessynicus* Becker, 1913 develop in the grass *Rottboellia* and rarely in the shoots of millets (Poaceae) and the third-instar larva (including the cephaloskeleton) and the puparium were described in detail by Deeming (1977). In the Afrotropics, the immature stages of two species are known to be primary invaders of plants and can cause economic damage to cultivated plants, these being gladioli (*Gladiolus* spp.) (Crocoideae) stems (the Gladioli fly, *Epimadiza hirta* Malloch, 1928) and seedlings of the Kapok tree, *Ceiba pentandra* (L.) Gaertn. (Malvaceae) (Cuthbertson 1935). *Epimadiza gallicola* Séguy, 1933 is thought to feed on decaying plant tissue (saprophagous) and has been found in galls on a shrub and on damaged cotton bolls (Ferrar 1987: 111). It has also been encountered in considerable numbers from fallen mahogany fruits damaged by a pyralid moth larva in Nigeria and from puparia in frass of the False codling moth, *Thaumatotibia leucotreta* (Meyrick, 1913) (Tortricidae) in citrus in Nigeria (Deeming & Al-Dhafer 2012). *Epimadiza nigrescens* Duda, 1933 was reared from millet heads, Sorghum shoots and decaying lettuce in Nigeria, all of which may have been damaged by other insects (Dawah *et al*. 2020). Deeming & Al-Dhafer (2012) described the puparium of *E. gallicola* and illustrated the prothoracic spiracle and cephaloskeleton.

Some species in *Gaurax* (as currently defined), have been recorded from fungi (Nartshuk 2012) and extralimital species from decaying plant material and insect egg masses (Ferrar 1987: 112). *Gaurax mycophagus* Nartshuk & Kurina, 2014 has been reared from fungi in central Benin (Nartshuk & Kurina 2014) and Smith (1965) described the posterior spiracle and puparium of the Palaearctic *G. dubius* (Macquart, 1835) that had been reared from bracket fungi (Polyporaceae), while it is not clear if the other figures included in Ferrar (1987: 614–622) are of true *Gaurax* species.

The immature stages of *Hapleginella* Duda have been recorded from conifer cones in the Nearctic and Palaearctic Regions (Ferrar 1987: 113) and the cephaloskeleton of the Palaearctic species *H. laevifrons* (Loew, 1858) was described by Gaidene & Nartshuk (1963) and was figured in Ferrar (1987: 618). Nartshuk (1987: 92, 97, 107) figured the larval pseudocephalon, the cephaloskeleton and the first and sixth abdominal segment of the larva of *H. laevifrons*. Deeming (1981a) described the puparium and cephaloskeleton of *Lagaroceras annulatum* Deeming, 1981, described the puparium of *L. pulchellum* Lamb, 1917 and figured the prothoracic puparial spiracles of *L. annulatum*, *L. pulchellum* and the Oriental species *L. tenuicorne* Malloch, 1927 and the cephaloskeleton of *L. pulchellum*.

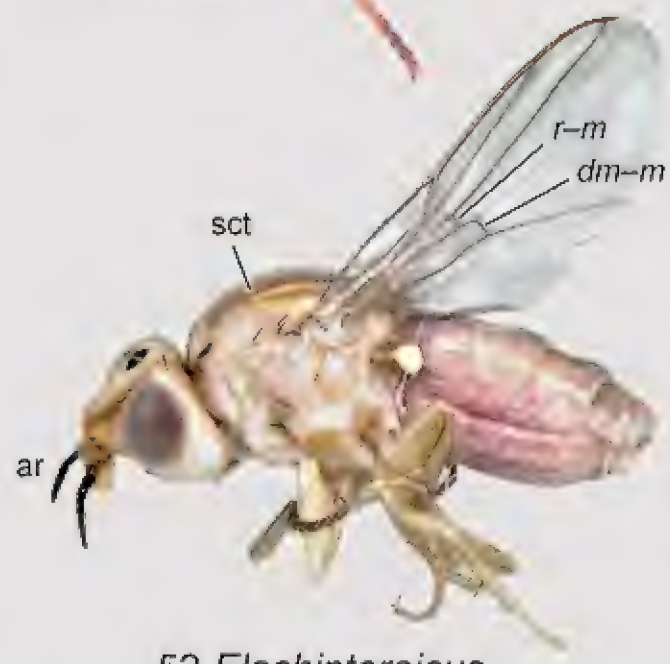
The life histories of *Lasiambia* Anonymous are poorly understood and varied. Some species have been recorded as egg predators of Orthoptera, from rotting sweet potato and from stems of *Conium* (Apiaceae) in Europe (Ferrar 1987: 112, as *Fiebrigella* Duda). Ferrar (1987: 613) illustrated the cephaloskeleton of *L. oophila* (Hennig, 1941). Nartshuk & Andersson (2013: 118) summarised the biology of the western Palaearctic species of *Lipara*, including the sound communication of adults and Grochowska (2013) and Waitzbauer (1969) provided detailed descriptions of all immature stages of the non-Afrotropical species *L. lucens*.

The immature stages of *Steleocerellus* Frey have been found in grasses and cereal crops (Deeming & Al-Dhafer 2012).



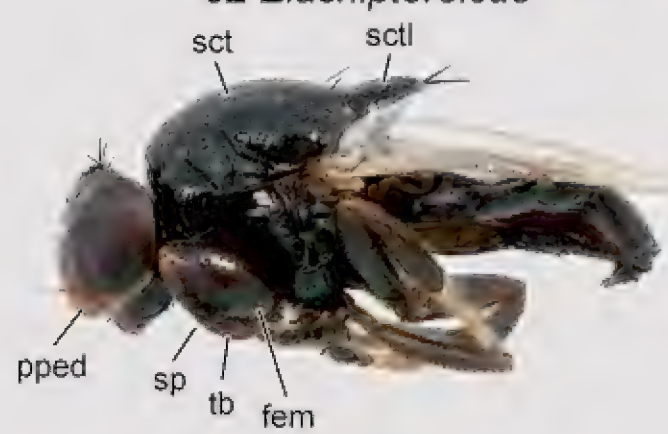
50 *Dicraeus*

51 *Diplotoxa* (*Diplotoxa*)

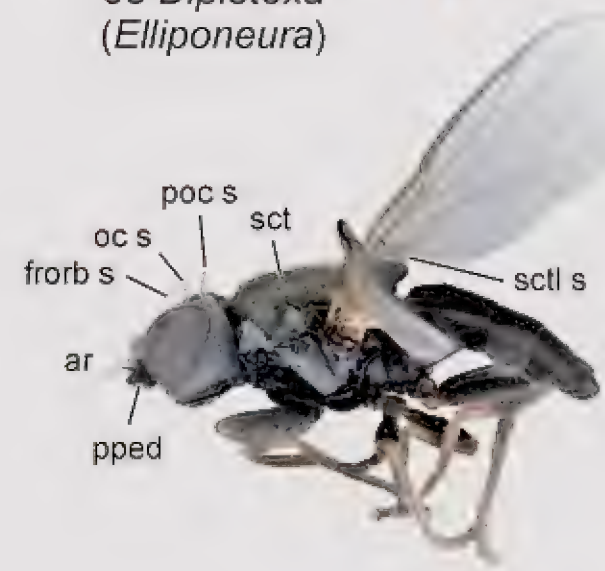


52 *Elachiptereicus*

53 *Diplotoxa* (*Elliponeura*)



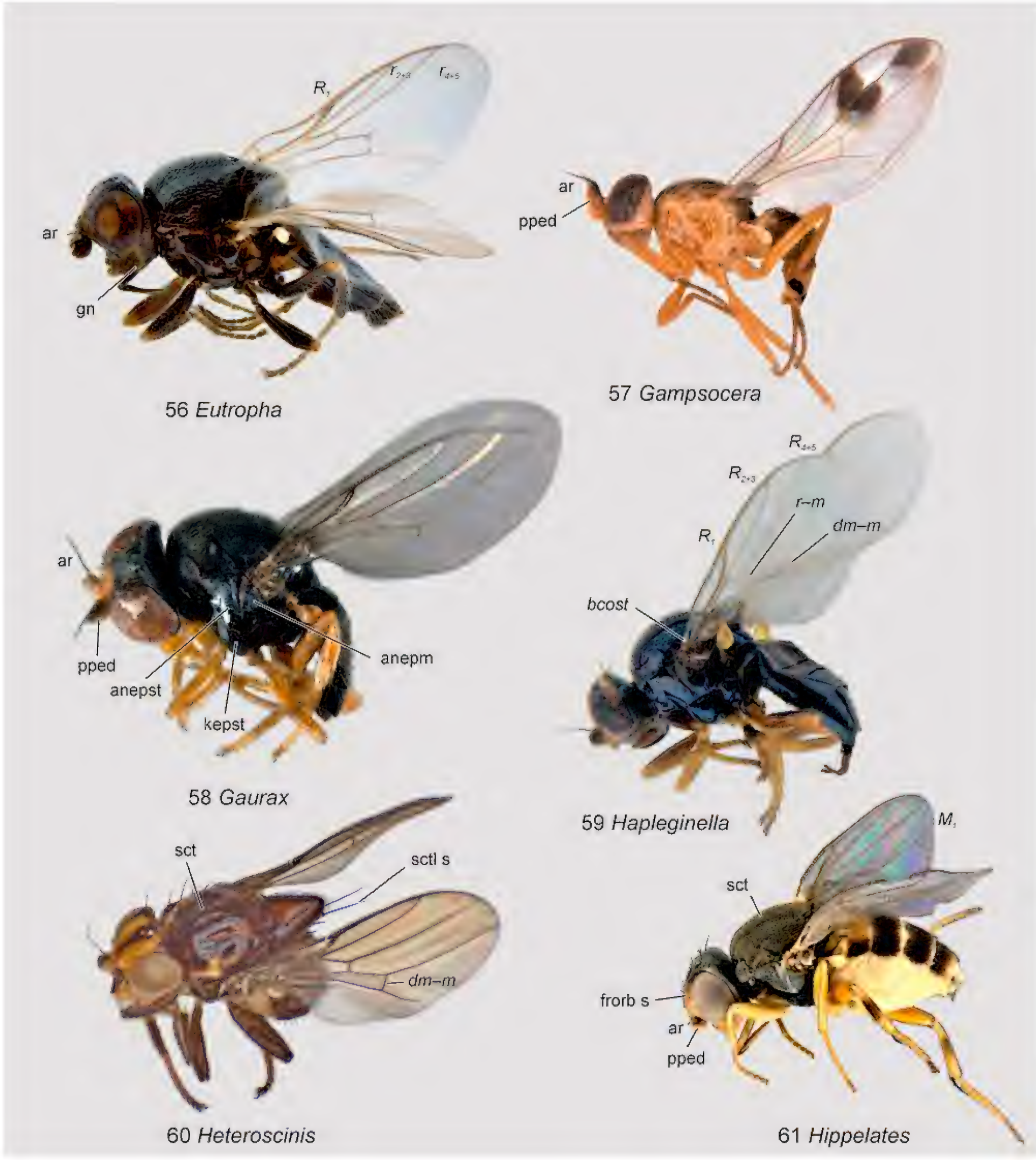
54 *Epimadiza*



55 *Eribolus*

Figs 96.50–55. Habitus of Chloropidae (lateral views): (50) *Dicraeus vagans* (Meigen) (non-Afrotropical); (51) *Diplotoxa* (*Diplotoxa*) *messoria* (Fallén) (non-Afrotropical); (52) *Elachiptereicus abessynicus* Becker; (53) *Diplotoxa* (*Elliponeura*) sp.; (54) *Epimadiza gallicola* Séguy; (55) *Eribolus* sp. Figs 51, 52, 54 (© National Museum of Wales).

Abbreviations: ar – arista; *bcost* – basicosta; *dm–m* – discal medial crossvein; fem – femur; frorb s – fronto-orbital seta; M_1 – first branch of media; oc s – ocellar seta; oc tr – ocellar triangle; poc s – postocellar seta; pped – postpedicel; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; sct – scutum; sctl – scutellum; sctl s – scutellar seta; sp – spine; tb – tibia.



Figs 96.56–61. Habitus of Chloropidae (lateral views): (56) *Eutropha lindneri* Sabrosky; (57) *Gampsocera* sp. (non-Afrotropical); (58) *Gaurax* sp. (non-Afrotropical); (59) *Hapleginella laevifrons* (Loew) (non-Afrotropical); (60) *Heteroscinis hystrix* (Séguy); (61) *Hippelates proboscideus* Williston.

Abbreviations: anepm – anepimeron; anepst – anepisternum; ar – arista; *bcost* – basicosta; *dm–m* – discal medial crossvein; frorb s – fronto-orbital seta; gn – gena; kepst – katepisternum; M_1 – first branch of media; pped – postpedicel; R_1 – anterior branch of radius; r_{2+3} – second + third radial cell; R_{2+3} – second branch of radius; r_{4+5} – fourth + fifth radial cells; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; sct – scutum; sctl s – scutellar seta.

Kirk-Spriggs (1986) provided detailed descriptions of the puparia, including the cephaloskeleton, of two West African *Mepachymerus* Speiser species and of three species of *Steleocerellus*. *Merochlorops flavipes* (Malloch, 1927) larvae have been reared from Ginger, *Zingiber officinale* Roscoe (Zingiberaceae) and *M. cardami* (Duda, 1935) larvae from Cardamom, *Elettaria cardamomum* Mato (Zingiberaceae), stem in India (Cherian 1991) and the puparium of *M. cardami* (a junior synonym of *M. flavipes* (Malloch, 1927) was described in the same paper. *Merochlorops flavipes* larvae are known to bore the stems of Cardamom and Ginger (Nartshuk *et al*. 2015). The Indian species *M. dimorphus* Cherian 1991 was investigated as a biocontrol agent of the invasive Ginger lily, *Hedychium gardnerianum* Sheppard ex J.B. Ker Gawler (Zingiberaceae) in India and in laboratory conditions in the United Kingdom (Djeddour *et al*. 2012) and this report included images of a larva, puparium and adult.

The green larvae of extralimital species of *Meromyza* are recorded as primary invaders of stems of grasses and cereals and can cause economic damage (Ferrar 1987: 116). Balachowsky & Mesnil (1935: 959) illustrated three Palaearctic *Meromyza* larvae. Deeming (2018) recorded the genus *Meromyzella* as being ovoviviparous. The immature stages of extralimital species of *Microcercis* Beschovski (as *Incertella* Sabrosky) are known from the stems of grasses and cereal crops (Nartshuk & Andersson 2013: 110) and Grochowska provided detailed descriptions of all immature stages of the non-Afrotropical species *M. zuercheri* (as *Incertella*) (Grochowska 2008a). Larvae of *Neoloxotaenia gracilis* (de Meijere, 1908) have been noted as developing in Cardamom in India (Deeming 2011: 802) and the species was reared from puparia from a shoot of the Ginger lily in Sikkim, India (Djeddour *et al*. 2012).

Larvae of some species of *Oscinella* are known to invade the stems of grasses, causing the meristem (the growing point of the shoot) to die and leading to economic damage to cereal and fodder crops, including millets, rice and Sorghum. Ferrar (1987: 113) gave a short summary of the biology of the genus, including an overview of larval hosts and feeding mechanisms and further references. Nartshuk & Andersson (2013: 124) included detailed information on the biology of some Palaearctic species and of *O. nitidissima* (Meigen, 1838) and commented on the *O.* (*Oscinella*) *frit* (L., 1758) complex. Deeming (2003) included a detailed description of the third-instar larva and puparium of *O.* (*Cyclocercula*) *nartshukiana* Beschovski, 1978, including figures of both subgenera and a detailed description of the puparium, including figures of the cephaloskeleton and prothoracic spiracle of *O. nitidigenis* (Becker, 1908). Balachowsky & Mesnil (1935) provided figures of larvae and pupae of three Palaearctic species of *Oscinella*, including a detailed description of *O.* (*O.*) *frit*. Ferrar (1987: 613) included figures of all immature stages, except the first-instar larvae and cephaloskeleton of *O.* (*O.*) *frit* and the third-instar larva and cephaloskeleton of the Palaearctic species *O. vastator* (Curtis, 1845). Nartshuk (1987: 87) provided detailed figures of immature stages of several species of *Oscinella*, including the third-instar larva and cephaloskeleton of the Afrotropical species *O. nitidissima* and Nartshuk & Andersson (2013: 134) illustrated the spicules on the ventral surface of the larva.

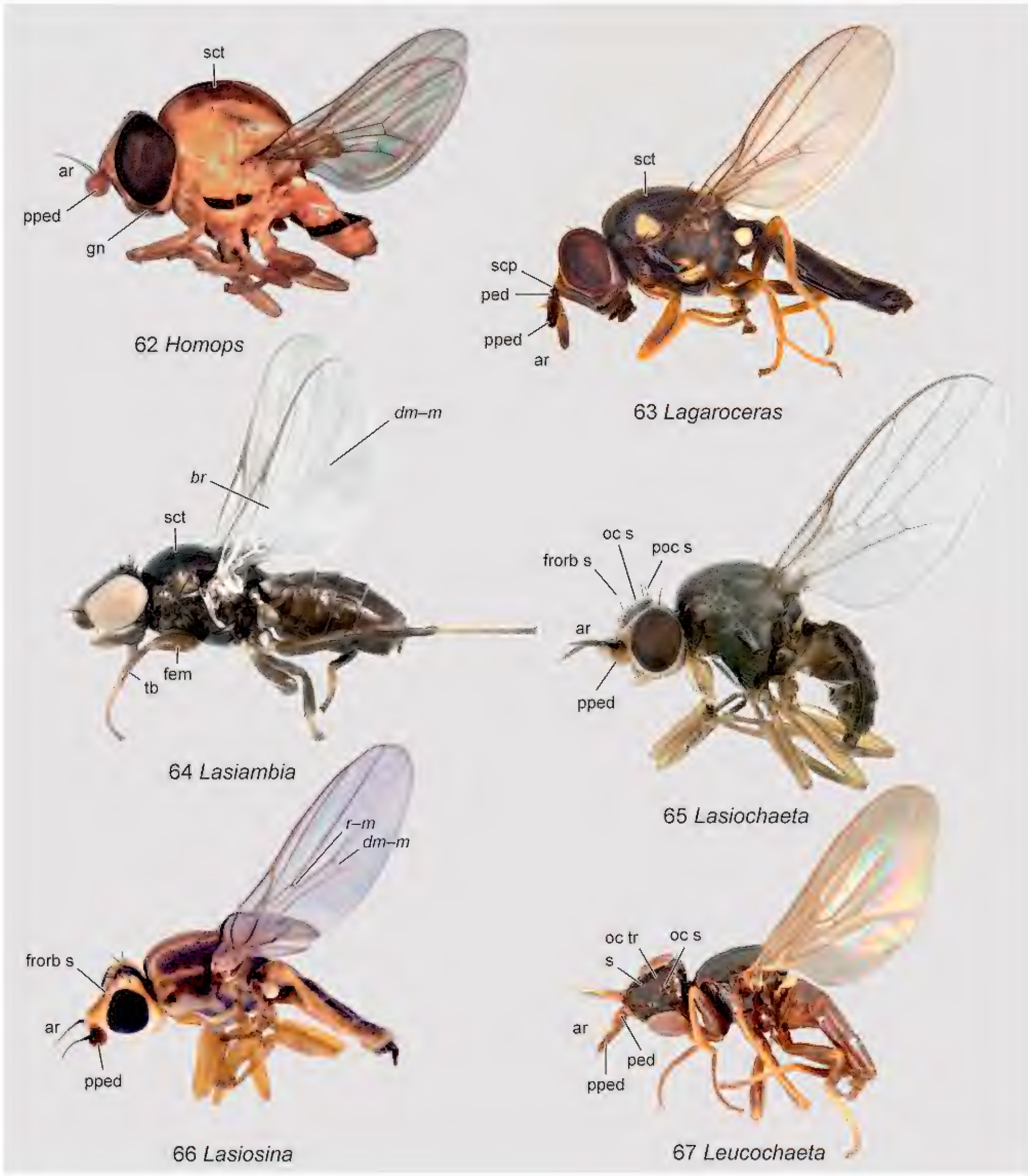
Pachylophus is ovoviviparous and larvae have been found in the stems of grasses and cereals including rice, but in many cases are thought to be secondary invaders after damage by other insects (Deeming 2018). Deeming (1974) described the third-instar larva and puparium of *Pachylophus beckeri*; Deeming (1977) the same for *P. lugens* Loew, 1860; and Spencer (1985: 79) figured the cephaloskeleton of *P. punctifemur* Sabrosky, 1945. *Parectecephala gigas* Sabrosky, 1951, was reared in Uganda from shoots of grasses (*Pennisetum* spp.) and the prothoracic spiracle and cephaloskeleton were described and figured (Deeming 1981a), while Sabrosky (1951: 737) described and figured the puparial posterior spiracle.

In the Palaearctic Region, larvae of some species of *Platycephala* Fallén bore the stems of Common reed, *Phragmites australis* (Cav.) Trin. ex Steud. (Poaceae) and can thus cause economic damage where the reed is grown commercially, or act as control agents where it is unwanted (B. & J.W. Ismay, pers. obs.). Grochowska (1991) described the immature stages of the Palaearctic species *P. planifrons* (F., 1798). The biology of *Polyodaspis* Duda is poorly known, but extralimital species have been recorded from a wide range of media, including other insects and plants (Ferrar 1987: 108). Deeming & Al-Dhafer (2012) illustrated the puparium and the larval cephaloskeleton of *P. picardi* Séguy, 1946; Nartshuk & Andersson (2013: 231) figured the third-instar larva, cephaloskeleton and spiracular zones of the Southern European walnut pest species *P. ruficornis* (Macquart, 1835).

The immature stages of *Pseudogampsocera scutellata* (Lamb, 1912) have been recorded from the grass *Stenotaphrum dimidiatum* (L.) Brongn. (Poaceae) by Sabrosky (1964). In the Afrotropics, larvae of *Pseudogaurax* are known to be predators of spider egg masses and mantid oothecae (Boulard *et al*. 1989; Cogan 1977). Asquith & Adamski (1989) described the third-instar larva of *P. signatus* (Loew, 1876), with detailed illustrations; Nartshuk & Andersson (2013: 231) figured the puparium of *P. chiyokae* Kanmiya, 1972; and larvae of extralimital species are known to also be predacious upon the egg masses of ants (Hymenoptera: Formicidae), Megaloptera and Orthoptera and to parasitise Lepidoptera larvae and pupae (Ismay & Ang 2019) and to develop in the egg masses of Amplypygi (Corey & Hebets 2017; Gillung & Borkent 2017; Viquez & De Armas 2009).

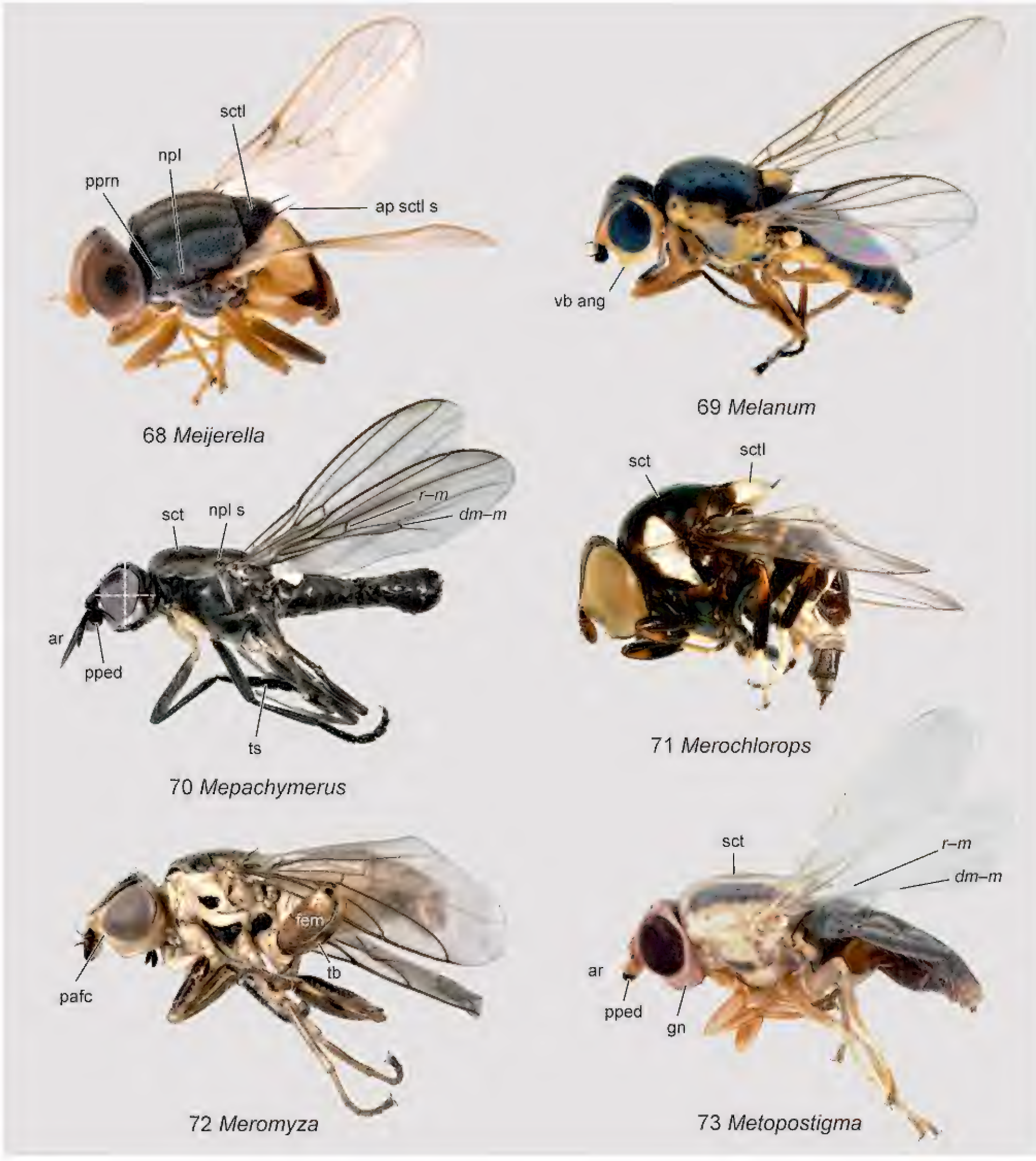
Rhodesiella formosa (Lamb, 1918) has been reared from the Gassa tree, *Manilkara butugi* Chiov. (Sapotaceae) in Kenya and some other species have been reared from damaged plant tissue in Papua New Guinea (J.W. Ismay, unpubl.) and twigs of Breadfruit trees, *Artocarpus altilis* (Parkinson) Fosberg (Moraceae), in Hawaii (Ferrar 1987: 114). The genus *Rhopalopterum* Duda has been reared from the stems of sedges in other regions (Nartshuk & Andersson 2013: 141). Larvae of the Nearctic species *R. atriceps* (Loew, 1863) (as *Stenoscinis atriceps*) have been recorded as secondary invaders of sedge stems attacked by the scathophagid *Cordilura varipes* (Walker, 1849) (Valley *et al*. 1969). Deeming (2018) recorded *Sabeurina* Deeming as ovoviviparous and commented briefly on the first-instar larvae.

In the Palaearctic, the immature stages of *Siphonella* Macquart have been found associated with spider egg masses (Ferrar 1987: 114), but Nartshuk & Andersson (2013: 145) considered this to be incorrect and recorded larvae feeding on coccids (Hemiptera: Sternorrhyncha) on grasses. In the United States, four adults were reared at the end of August from a spider egg-sac (Coquillett 1898: 75). *Siphunculina* has been reared from mud



Figs 96.62–67. Habitus of Chloropidae (lateral views): (62) *Homops* sp.; (63) *Lagaroceras pulchellum* Lamb; (64) *Lasiambia albidipennis* (Strobl); (65) *Lasiochaeta vulgaris* (Adams); (66) *Lasiosina* sp.; (67) *Leucochaeta trapezina* Becker. Fig. 62 (© Trustees of Natural History Museum, London), Figs 64, 65 (© National Museum of Wales), Fig. 67 (courtesy Y. Ang).

Abbreviations: ar – arista; *br* – basal radial cell; *dm–m* – discal medial crossvein; fem – femur; frorb s – fronto-orbital seta; gn – gena; oc s – ocellar seta; oc tr – ocellar triangle; ped – pedicel; poc s – postocellar seta; pped – postpedicel; *r–m* – radial–medial crossvein; s – setula; scp – scape; sct – scutum; tb – tibia.



Figs 96.68–73. Habitus of Chloropidae (lateral views): (68) *Meijerella inaequalis* (Becker); (69) *Melanum laterale* (Haliday) (non-Afrotropical); (70) *Mepachymerus lentus* (Curran) (length and depth of head indicated with dashed lines); (71) *Merochlorops ceylonica* (Duda); (72) *Meromyza nigriventris* Macquart (non-Afrotropical); (73) *Metopostigma* sp. Figs 70–73 (© National Museum of Wales).

Abbreviations: ap sctl s – apical scutellar seta; ar – arista; *dm–m* – discal medial crossvein; fem – femur; gn – gena; npl – notopleuron; npl s – notopleural seta; pafc – parafacial; pped – postpedicel; pprn– postpronotum; *r–m* – radial–medial crossvein; sct – scutum; sctl – scutellum; tb – tibia; ts – tarsus; vb ang – vibrissal angle.

(Syddiq 1938), mammal and bird dung and droppings (Kanmiya 1983) and adults are eye gnats, attracted to human and animal eyes in the Australasian and Oriental Regions and in Egypt, being implicated in the transmission of diseases of humans and other mammals, including livestock; the adults have also been reported from wounds. *Speccafrons* Sabrosky has been reared from spider egg masses (Nartshuk & Andersson 2013).

The immature stages of *Stenophthalmus* Becker have been reared from the shoots of cultivated Maize (*Zea mays* L.), millets, Sorghum, Sugarcane, *Saccharum officionarum* L. (Poaceae) and grasses (Deeming & Al-Dhafer 2012) and Deeming & Al-Dhafer (2012) described the puparium and illustrated the cephaloskeleton of *S. occidentalis* Deeming & Al-Dhafer, 2012. In Nigeria, *Stenoscinis arnos* Malloch, 1929, has been reared from shoots of Southern cut grass, *Leersia hexandra* Swartz (Poaceae) (J.C. Deeming, unpubl.), which is a serious weed pest of rice and a pest of Maize and Sugarcane (CABI 2020).

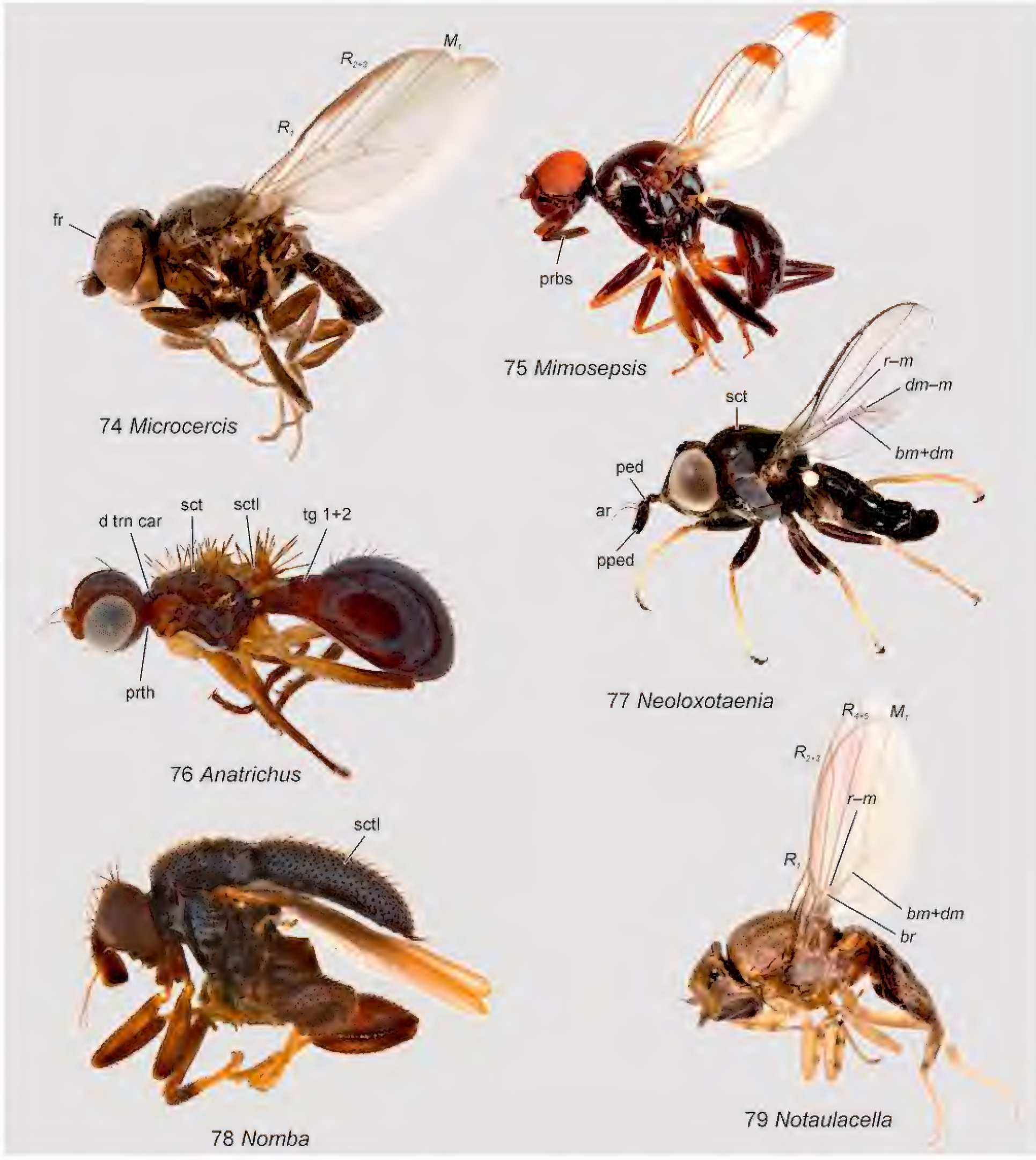
The immature stages of *Strobliola* Czerny have been recorded from grasses and cereal crops, including Maize, millets, Sorghum, Sugarcane and Wheat (Deeming 1972: 21; Deeming & Al-Dhafer 2012; Ismay 1998; Kanmiya 1983: 151). Deeming & Al-Dhafer (2012) described and illustrated the puparium of *S. flavofacies* and Ismay (1998) described part of the puparium. Larvae of extralimital *Thaumatomyia* Zenker are predatory on Hemiptera: Sternorrhyncha (Ferrar 1987: 107) and Balachowsky & Mesnil (1935: 976) illustrated the larva, the larval pseudocephalon and the posterior spiracle of *T. glabra* (Meigen, 1830).

Adults of extralimital *Trachysiphonella* Enderlein have been recorded in participating in the ant-meal of a spider (Harkness & Ismay 1975), or as obligatory pollinators of Apocynaceae or Birthwort (*Aristolochia* spp.) (Oelschlägel *et al*. 2014). The female flies are attracted to plant-produced odours, mimicking the often poisonous haemolymph of crushed or pre-digested arthropods after capture by predators. Nothing is known about larval substrates in this complicated system. The fly's eggs appear to carry the foul-smelling repellent. Larvae of extralimital *Tricimba* have been recorded from a variety of media, including decaying vegetable matter, fungi and spider egg masses (Ferrar 1987: 115; Ismay 1993). Ferrar (1987: 616, 619, 620, 622) illustrated the third-instar larva and provided details and the puparium of the Australian species *T. steatodae* Hickman, 1971 and Ismay (1993) figured the puparium in detail, the cephaloskeleton and the posterior spiracles of the puparium of *T. cardamomi* Ismay, 1993.

An excellent résumé of chloropid larval biology was provided by Ferrar (1987: 106). Balachowsky & Mesnil (1935) included numerous Chloropidae in their compendium of pest species. Nartshuk (2014) gave an excellent summary of the diversity, habitats and feeding strategies of chloropid larvae, Nartshuk & Andersson (2013) included host-plants and other natural history of Palaearctic genera and species (some of which also occur in the Afrotropics) and Tschirnhaus (1981) presented the results of a large study on Chloropidae, including rearing records. Valley *et al*. (1969) discussed the larval feeding habits of 26 species of Chloropidae from North America and Nye (1958) presented host-plant data and larval descriptions for some Palaearctic species. Many species occur as larvae in decaying vegetable matter, often associated with the attack of other insects (Ferrar 1987: 107; Grochowska 2011: 114) and it is difficult to decide whether a species is a primary invader of plant tissue or a scavenger following damage by another insect, which could also be a chloropid. Primary invaders are commonly found in grasses (Poaceae) and sedges (*Carex* spp.) (Cyperaceae), where larvae invade the whorl and destroy the meristem, causing the plant to develop a "dead heart", hence the vernacular name of "shoot flies". The bacteria in the rotting tissue of the meristem may comprise the nutrition for later larval instars (Ryzhkova 1962). Many genera are shoot flies of cereal crops and grasses and of these *Chlorops* and *Oscinella* are best known for the damage their larvae cause (Nartshuk 2014). Species known to be primary attackers of shoots frequently occur as secondary invaders of shoots already attacked by *Atherigona* Rondani (Muscidae) larvae and those of lepidopterous stem-borers. This is particularly so in the genus *Scoliophthalmus*, which will attack Sorghum in the rainy season before *Atherigona* has emerged, but appears to be a secondary invader once *Atherigona* is causing the primary attack (Deeming 1972: 7). It is not clear how much damage is done by *Scoliophthalmus* as a primary invader and further research on this topic is needed. *Dicraeus* larvae feed on the developing seeds (caryopses) of grasses and cereals at the milky grain stage, severely reducing grain yields in crops (Deeming 1979). Some species cause substantial galls to develop (*Lipara* and non-Afrotropical *Pseudeurina* de Meijere), which may have an association with other insects, including Chloropidae occurring as parasitoids or inquilines in the gall (Grochowska 2011: 92). Species of *Cryptonevra* and *Microcercis* (as *Incertella*) are frequently reared as inquilines in such galls (Grochowska 2011: 92). Some Chloropidae are primary invaders of fungal fruiting bodies (*Gaurax* and *Tricimba*) (Ferrar 1987: 106; Nartshuk & Kurina 2014). *Thaumatomyia* larvae prey upon root aphids (Fitch 1872; Nartshuk & Andersson 2013: 227). Some Chloropidae larvae cause leaf stem mines in higher plants (e.g., *Elachiptera megaspis* (Loew, 1858)) and in Watercress, *Nasturtium officinale* W.T. Aiton (Brassicaceae) (Uffen & Chandler 2010: 464).

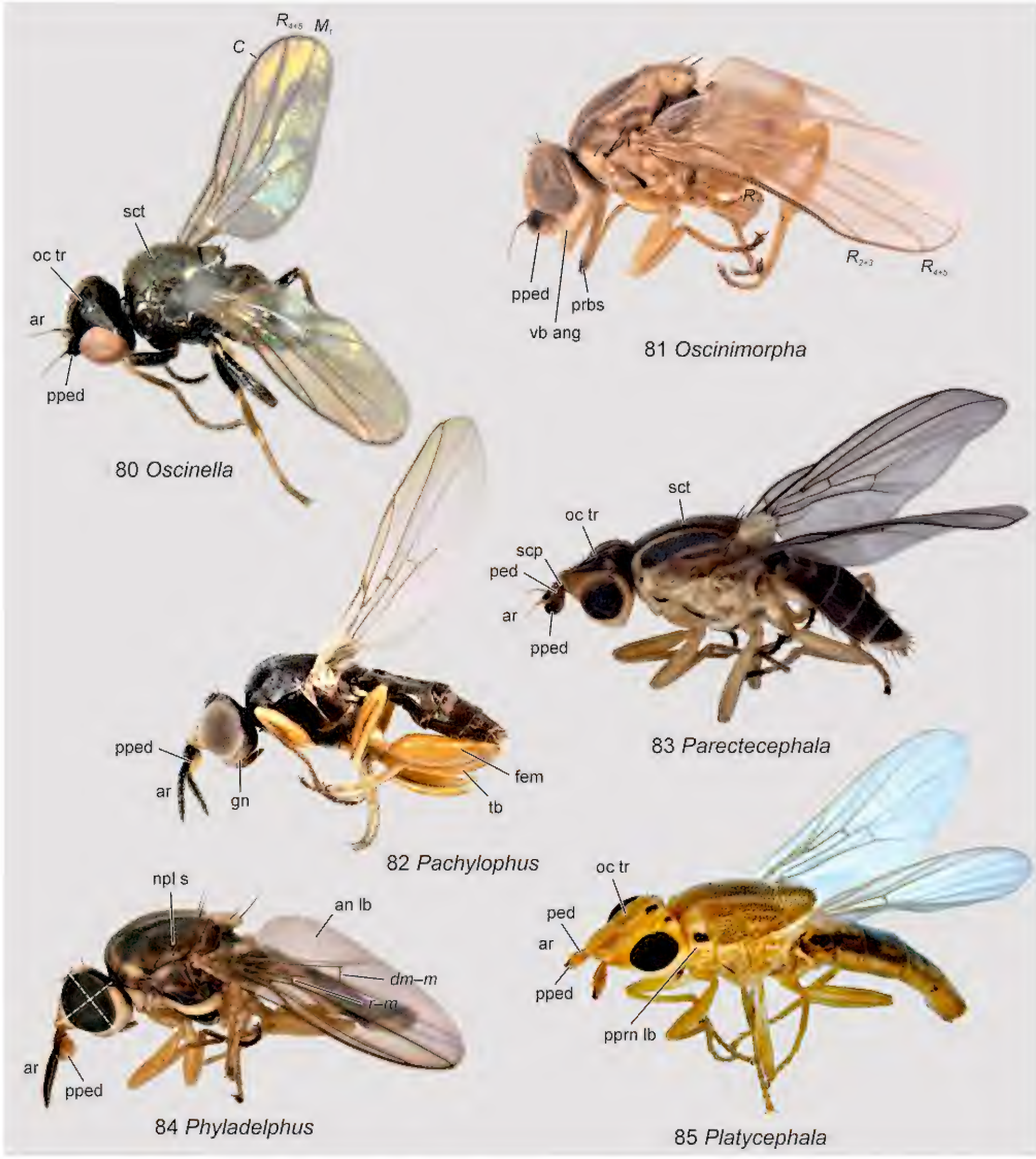
Several genera also have parasitic or predatory larvae. The Australian and Papua New Guinean genus *Batrachomyia* Krefft, has larvae that are subdermal parasites of frogs (Evenhuis 2006; Marshall 2012: 370), feeding on blood tissue (Kraus 2007). They appear to be host-specific, with individual species parasitising species from five different frog families (Kraus 2007). Some species appear to lower the fitness of the host species (Lemkert 2000; Schell & Burgin 2001), while others do not seem to have an effect at all (Kraus 2007; Lemkert 2000). No *Batrachomyia* species actively kill their hosts as this would be detrimental to the fly, which feeds on blood tissue and this is a different life-strategy to parasitic species in other Diptera families (Kraus 2007). *Batrachomyia* oviposit on moist substrates and the early stage larvae then enter the host, where they often develop under various glands (Kraus 2007).

Speccafrons larvae develop in spider egg-sacs, feeding on the developing eggs (Sabrosky 1980*a*) and larvae of the genera *Gaurax*, *Oscinimorpha* Lioy, *Siphonella* and *Tricimba* are also recorded as developing in spider eggs (Boulard *et al*. 1989). *Pseudogaurax* species have been reared from spider egg-sacs, mantid oothecae, Dobson fly eggs (Megaloptera), ant larvae (Formicidae) and Lepidoptera pupae (Boulard *et al*. 1989;



Figs 96.74–79. Habitus of Chloropidae (lateral views): (74) *Microcercis dimorphica* Deeming; (75) *Mimosepsis scutellaris* Deeming; (76) *Anatrichus* (formerly *Myrmecosepsis* Becker) sp.; (77) *Neoloxotaenia gracilis* (de Meijere); (78) *Nomba* sp.; (79) *Notaulacella* sp. Fig. 75 (© Trustees of Natural History Museum, London), Fig. 77 (© National Museum of Wales).

Abbreviations: ar – arista; *bm+dm* – basal medial cell + discal medial cell; *br* – basal radial cell; d trn car – dorsal transverse carina; *dm–m* – discal medial crossvein; fr – frons; M_1 – first branch of media; ped – pedicel; pped – postpedicel; prbs – proboscis; prth – prothorax; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; sct – scutum; sctl – scutellum; tg – tergite.



Figs 96.80–85. Habitus of Chloropidae (lateral views): (80) *Oscinella* sp.; (81) *Oscinimorpha* sp.; (82) *Pachylophus gallagheri* Deeming; (83) *Parectecephala gigas* Sabrosky; (84) *Phyladelphus geminus* Becker (length and depth of head indicated with dashed lines); (85) *Platycephala scapularum* (Becker).

Abbreviations: an lb – anal lobe; ar – arista; C – costal vein; *dm–m* – discal medial crossvein; fem – femur; gn – gena; M_1 – first branch of media; npl s – notopleural seta; oc tr – ocellar triangle; ped – pedicel; pped – postpedicel; pprn lb – postpronotal lobe; prbs – proboscis; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; scp – scape; sct – scutum; tb – tibia; vb ang – vibrissal angle.

Ismay & Ang 2019) and (non-Afrotropical) *Kurumemyia* Kanmiya from mantid oothecae (Kanmiya 1983). In the Palaearctic Region, grasshopper eggs are preyed upon by the larvae of *Lasiambia palposa* (Fallén, 1820) (Nartshuk & Andersson 2013: 116; Tschirnhaus 1992) and *L. coxalis* (von Roser, 1840) (Hennig 1941; Nartshuk & Andersson 2013: 116) and *Dysartia latigena* Sabrosky, 1991 is a larval predator of grasshopper eggs in the Nearctic Region (Sabrosky 1991). Several of these species oviposit on the outside of egg cases and the larvae then burrow through the covering and feed on the eggs.

Cadrema appears to be highly varied in its larval biology, having been reared from such diverse media as aphid (Aphididae) honeydew (which contains all the organic debris deposited on it by wind and developing fungi), stranded marine Mollusca and having passed alive through the human gut, feeding on the bowel contents (Bohart & Gressitt 1951; Ferrar 1987: 108). *Eugaurax setigena* Sabrosky, 1971 is a stem-miner of Water hyacinth, *Pontederia crassipes* Mart. (Pontederiaceae) in the Nearctic and Neotropical Regions (Sabrosky 1971). In the Neotropics, *Hippelates* Loew and *Liohippelates* Duda develop in Sugarcane refuse that has been ploughed into the soil (Tondella *et al*. 1994).

There is little information in the literature on mating behaviour in Chloropidae. *Epimadiza fascipennis* Sabrosky, 1945, has been observed running on tree trunks and waving its wings (Deeming & Al-Dhafer 2012), which are distinctively marked. Males of *Thaumatomyia notata* have been noted circling stationary females and everting their abdominal sacs, presumably producing pheromones (Kotrba 2009; Nartshuk 2000*b*); similar mating behaviour was observed in the Nearctic *Chaetochlorops inquilinus* (Coquillett, 1898) (Steyskal 1942). In Japan, Kanmiya (1981) has recorded *Lipara* species stridulating on reeds, producing a distinctive "song" differing between species and sexes and there are even regional "dialects". Grochovska (2011: 105) studied the development of *Lipara* species in great detail and showed that if two species occupy the same Common reed stem, only one survives; either the primary gall causer or the secondary inquiline (*e.g.*, *L. lucens* or *L. rufitarsis* Loew, 1858). A male swarm of *Homops madagascariensis* (Enderlein, 1911) has been observed, hovering about two metres above the ground in sunlight at Merrivale, South Africa (Deeming & Al-Dhafer 2012). The males of this species have an entirely white abdomen, while the females have the abdomen black and yellow banded; indicating that this is probably a mating swarm, with the male abdominal colour enticing females to enter. Most species of Chloropidae do not exhibit sexual dimorphism.

Nartshuk (2014) summarised egg-laying behaviour in many genera and species, including *Chloropsina citrivora* Sabrosky, 1976, a pest of *Citrus* (Rutaceae). She also mentioned the modified, sclerotised ovipositors of some species. Deeming (2018) discussed ovoviviparity in Chloropidae, where only one ovariole is developed and a single egg is produced and hatches, the larva being laid when almost mature and pupariating within the host-plant (Pollock 1996: 183).

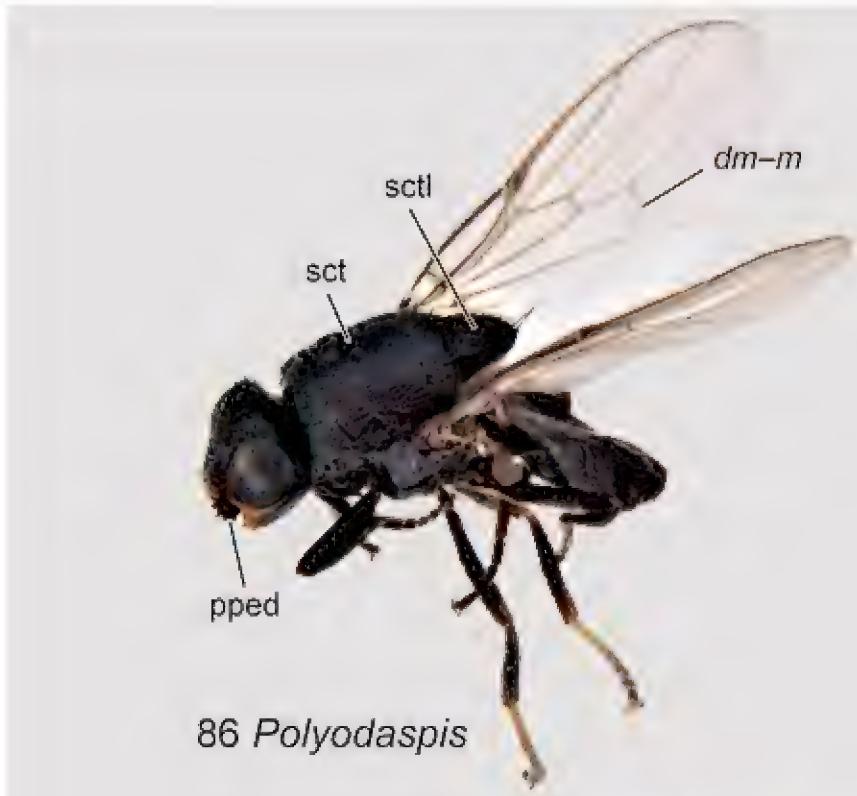
Economic significance

The Chloropidae include many species that are major pests of crops, such as *Dicraeus*, *Oscinella* and *Pachylophus*, therefore it is not surprising that they have a major impact on agriculture and health. They are known as vectors of several diseases, some are important agricultural pests by damaging food crops or pastures, while others can make human habitations uninhabitable due to mass occurrence. Chloropidae are also known as important pollinators and potential biocontrol agents of plants or invertebrates. Their importance in some of these areas is poorly known, however, and requires further investigations.

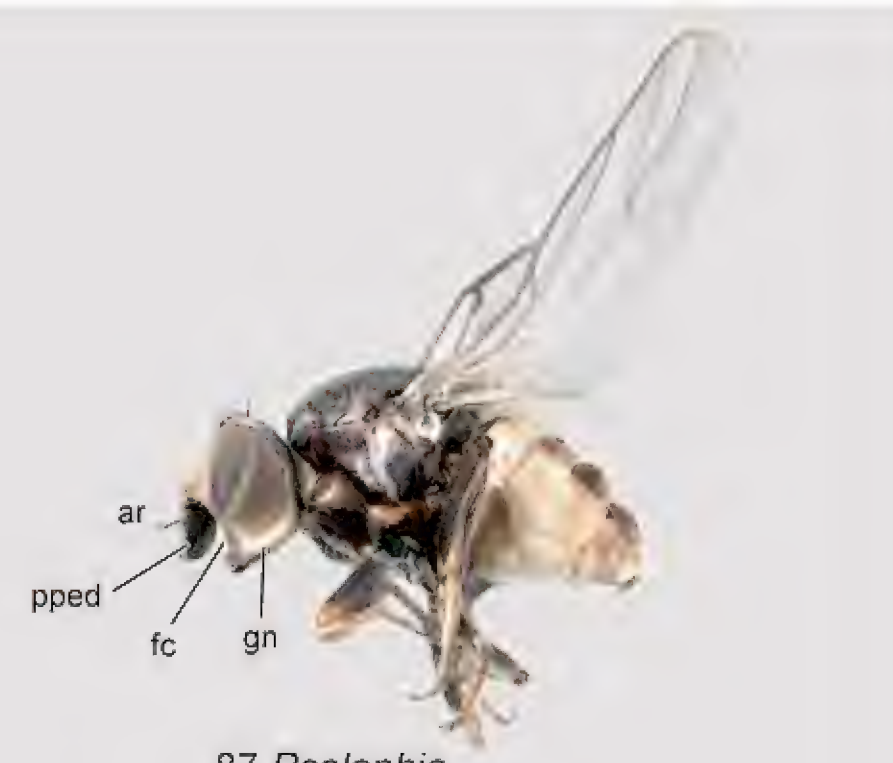
The adults of some species of *Hippelates*, *Liohippelates* and *Siphunculina* feed on lacrimal and sebaceous fluids at the eyes of humans (Marshall & Kirk-Spriggs 2017: 144) and have been recorded as vectors of the pathogens of conjunctivitis and Brazilian purpuric fever (Tondella *et al*. 1991, 1994), with the latter disease notorious in child deaths. Adults of *Liohippelates flavipes* (Loew, 1866) have also been recorded as being attracted to the lesions of yaws and are implicated in the transmission of that disease (Sabrosky 1974). The bacteria that cause acute conjunctivitis (pink eye or sore eye) are transmitted by several species of *Hippelates*, *Liohippelates* and *Siphunculina* (Chansang *et al*. 2010, 2011; Kanmiya 1989; Mulla & Chansang 2007; Sathe & Jadav 2014) and *Sabroskyina aharonii* (Duda, 1933) (Machtinger & Kaufman 2018; Rogoff 1978: 52). In the Oriental Region, *Siphunculina* species are regarded as serious pests, as they transmit bacteria causing pink eye to humans and livestock (Sathe & Jadav 2014) and they have also been implicated in causing septicaemia, by transmitting relevant bacteria (Chansang *et al*. 2010). In the Neotropics, *Liohippelates* is implicated in the transmission of the bacterium *Haemophilus influenzae* biotype *aegyptius* (Pasteurellaceae), which causes Brazilian purpuric fever, notorious in child deaths (Cury *et al*. 2014; Machtinger & Kaufman 2018; Tondella *et al*. 1994).

Yaws and pinta, both diseases that affect humans in poorer parts of the tropics, are caused by the bacteria *Treponema pertenue* Castellani and *T. carateum* Brumpt (Spirochaetaceae), respectively. These diseases are known to be transmitted during the rainy season by *Liohippelates flavipes* and *L. pallipes* (Loew, 1863) (Greenberg 1973: 23). Yaws also causes economic losses to the livestock industry (Kumm 1935; Kumm & Turner 1936; Machtinger & Kaufman 2018; Morgan 2011; Saunders *et al*. 1936), with the pathogen transmitted to livestock by *L. apicatus* (Malloch, 1913) (as *Hippelates illicis*), *L. currani* (Aldrich, 1931), *L. flavipes*, *L. peruanus* (Becker, 1912) and *L. pusio* (Loew, 1872) (Greenberg 1971: 230).

Greenberg (1971: 229) listed the bacterial pathogen *Treponema carateum*, which is agent of the infectious tropical disease pinta, in a *Hippelates* sp. in the tropics. It appears that several species may have been misidentified, however and that transmission may thus be possible by various species of *Hippelates/Liohippelates*. The pathogens of acute bovine mastitis are transmitted by *Liohippelates* species in the warmer parts of the Nearctic and Neotropical Regions (Sanders 1940) and the genus is also instrumental as a vector of vesicular stomatitis, a viral disease that causes lesions on cattle, goats, pigs and sheep (Machtinger & Kaufman 2018). *Liohippelates* species also cause economic losses to livestock, due to their sheer numbers, causing the panic behaviour known as "gadding" (Hinkle *et al*. 2001). All eye gnats (*Liohippelates*, *Hippelates*, *Siphunculina* and *Sabroskyina* Beschovski), are attracted to the orifices,



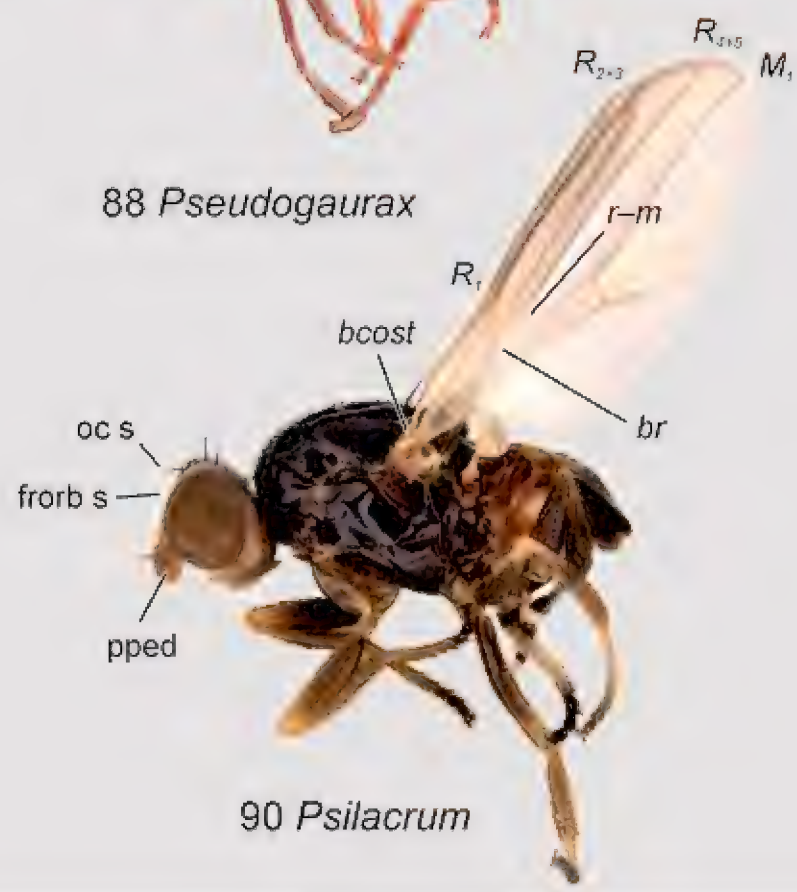
86 *Polyodaspis*



87 *Pselaphia*

88 *Pseudogaurax*

89 *Diplotoxa* (*Pseudopachychaeta*)

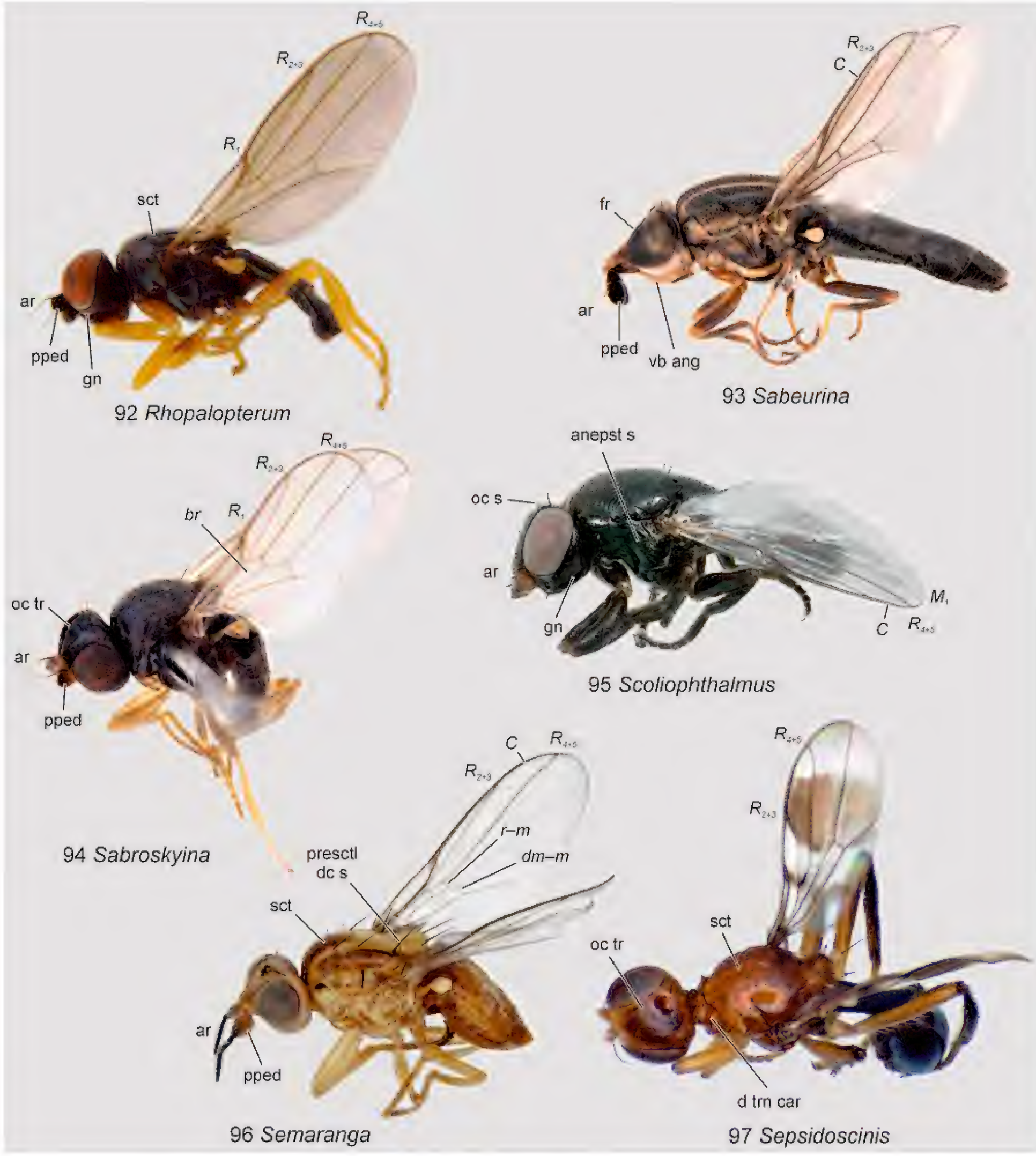


90 *Psilacrum*

91 *Rhodesiella*

Figs 96.86–91. Habitus of Chloropidae (lateral views): (86) *Polyodaspis ruficornis* (Macquart) (non-Afrotropical); (87) *Pselaphia cornifera* Becker; (88) *Pseudogaurax sicarius* (Lamb); (89) *Diplotoxa* (*Pseudopachychaeta*) *ruficeps* (Zetterstedt) (non-Afrotropical); (90) *Psilacrum* sp.; (91) *Rhodesiella* sp. Figs 87, 88 (© National Museum of Wales).

Abbreviations: ap sctl s – apical scutellar seta; ar – arista; *bcost* – basicosta; *br* – basal radial cell; C – costal vein; *dm–m* – discal medial crossvein; fc – face; gn – gena; frorb s – fronto-orbital seta; M_1 – first branch of media; M_4 – fourth branch of media; oc s – ocellar seta; pped – postpedicel; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; sct – scutum; sctl – scutellum.



Figs 96.92–97. Habitus of Chloropidae (lateral views): (92) *Rhopalopterum atricorne* (Zetterstedt) (non-Afrotropical); (93) *Sabeurina minuta* (Loew); (94) *Sabroskyina aharonii* (Duda); (95) *Scoliophthalmus trapezoides* Becker; (96) *Semaranga dorsocentralis* Becker; (97) *Sepsidoscinis maculipennis* Hendel (non-Afrotropical). Fig. 95 (© National Museum of Wales).

Abbreviations: anepst s – anepisternal setulae; ar – arista; *br* – basal radial cell; *C* – costal vein; d trn car – dorsal transverse carina; *dm–m* – discal medial crossvein; fr – frons; gn – gena; M_1 – first branch of media; oc s – ocellar seta; oc tr – ocellar triangle; pped – postpedicel; presctl dc s – prescutellar dorsocentral seta; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; sct – scutum; vb ang – vibrissal angle.

including eyes, nose and lips and/or to open wounds in humans and livestock, thus enabling the transmission of the vectors of these diseases. Rogoff (1978: 52) summarised the role of all eye gnats as vectors and outlined methods for their collection.

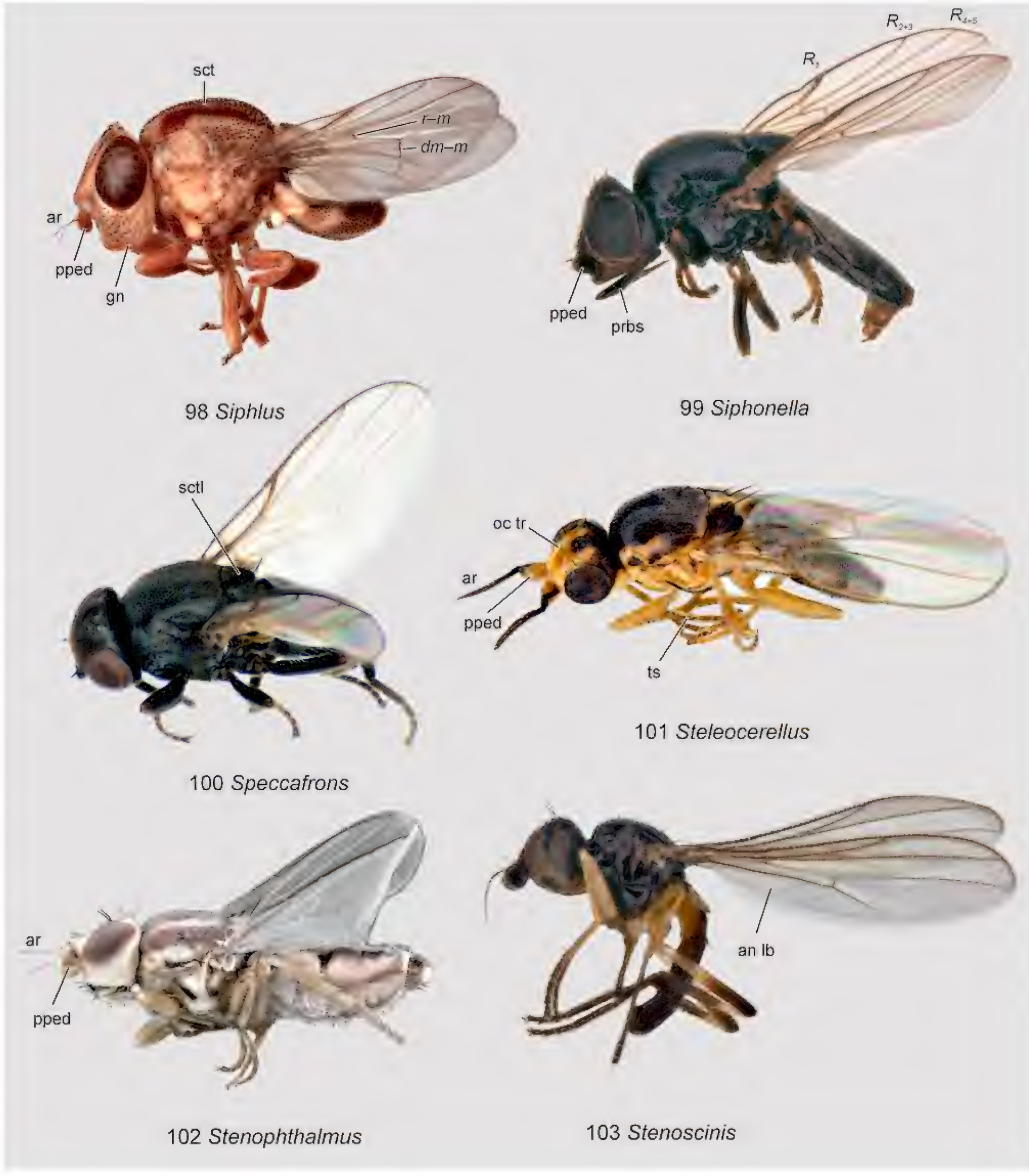
Myiasis in frogs in Australia is caused by *Batrachomyia*. Flies oviposit on damp substrates and larvae actively seek out their hosts and upon location burrow into the skin. There they develop in subcutaneous lymph spaces, feeding on blood and the third-instar larvae breathe with their posterior spiracles through an opening in the host's skin. Upon maturation, the larvae exit the frog and pupariate in dark spaces. It is estimated that 10% of hosts die when larvae emerge (Zumpt 1965: 30), but death may be due to secondary infections, as both Kraus (2007) and Lemkert (2000) did not find a reduced or only very minimal reduced fitness in frog species.

Rice is attacked by several Chloropidae species, including *Pachylophus beckeri*, widespread in the Afrotropics (Deeming 2018). It attacks cultivated African rice (*Oryza glaberrima* Steud.), Asian rice (*O. sativa* L.) and African wild rice (*O. barthii* A. Chev.) (Poaceae), as a shoot fly (Deeming 1974; Heinrichs & Barrion 2004: 34; Moyal 1982), where it destroys the meristem of the stem, which eventually dies and decays. *Pachylophus beckeri* has a unique adaptation of the puparium to prevent it from drowning if the crop is inundated. Upon pupariation the larval prothoracic spiracles migrate onto its ventral surface and penetrate the aerenchyma of the adjacent leaf, facilitating the pupa deriving oxygen directly from the host-plant (Deeming 1974). *Chlorops oryzae* Matsumura, 1915, attacks rice in the Oriental Region (Kanmiya 1983). Other species reared from rice (cultivated or African wild rice) in the Afrotropical Region are: *Anatrichus erinaceus* Loew, 1869, *A. pygmaeus* Lamb, 1918, *Mepachymerus baculus* Speiser, 1910, *Oscinella* (*Cyclocercula* Beschovski) *nartshukiana*, *Scoliophthalmus micantipennis* Duda, 1935 and *S. trapezoides* Becker, 1903 (Deeming 2003; Deeming & Al-Dhafer 2012; Ferrar 1987: 107, 116; Kirk-Spriggs 1986; Nartshuk 2004), although further research is required to establish if *A. erinaceus*, *A. pygmaeus* and *M. baculus* are primary (meaning damaging) or secondary invaders, in the case of *A. pygmaeus* Lamb, 1918 (Wongsiri *et al*. 1974) and *M. baculus* moving into damage caused by other insect species. According to Gautam *et al*. (2009), *A. erinaceus* caused serious damage to Basmati rice (variety) in four districts in India as a primary invader. *Mepachymerus baculus* is considered to be a predator of Diopsidae larvae occurring as pests in rice stems (Descamps 1957: 141, as cited in Deeming 1981), but further investigation is required to determine whether the species is a necrophage (feeding on dead bodies) or a predator.

Several millet species are known to host chloropid larvae, whether as primary damagers or secondary invaders is not known in all cases and requires further research. This is particularly important, as millets are often grown in very arid conditions and are becoming more important food plants in the Sahel zone of Africa. Pearl millet, *Pennisetum glaucum*, is attacked by the Seed fly, *Dicraeus pennisetivora*, which is widespread in West Africa and can cause significant loss in yields (Deeming 1979). Another species that damages millet shoots (Pearl millet, Finger millet, *Eleusine coracana* Gaertn. and Napier grass, *P. purpureum* Schumacher), is *Oscinella* (*C.*) *nartshukiana* (Deeming 1971, 2003). The primary invaders (damagers) *Scoliophthalmus trapezoides* and *S. micantipennis* are common in Africa south of the Sahara and have been reared from Pearl millet and Napier grass (Deeming 1972: 10; Deeming & Al-Dhafer 2012). *Strobliola flavofacies* is common in Nigeria and damages millets in the latter half of the rainy season and on irrigated plots during the dry season (Deeming 1972: 12). Common millet or Proso millet, *Panicum miliaceum* L., is damaged in the United States by *Meromyza americana* Fitch, 1856, the larvae of which feed within the stem near the upper node and cause whiteheads (Kalaisekar *et al*. 2016: 19). The following species have been reared from a millet species, but it has not been established if these are primary or secondary invaders and further research is required: *Anacamptoneurum obliquum* Becker, 1903, *Anatrichus pygmaeus*, *Steleocerellus latiseta* (Lamb, 1917), *S. tenellus* (Becker, 1910), *Scoliophthalmus trapezoides* and *Strobliola flavofacies* (Deeming 1972: 10; Deeming & Al-Dhafer 2012; Kirk-Spriggs 1986). *Anthracophagella albovariegata* (Thomson, 1869) has been reared from the drought resistant Kodo millet (*Paspalum scrobiculatum* L.) (Deeming 1981*a*).

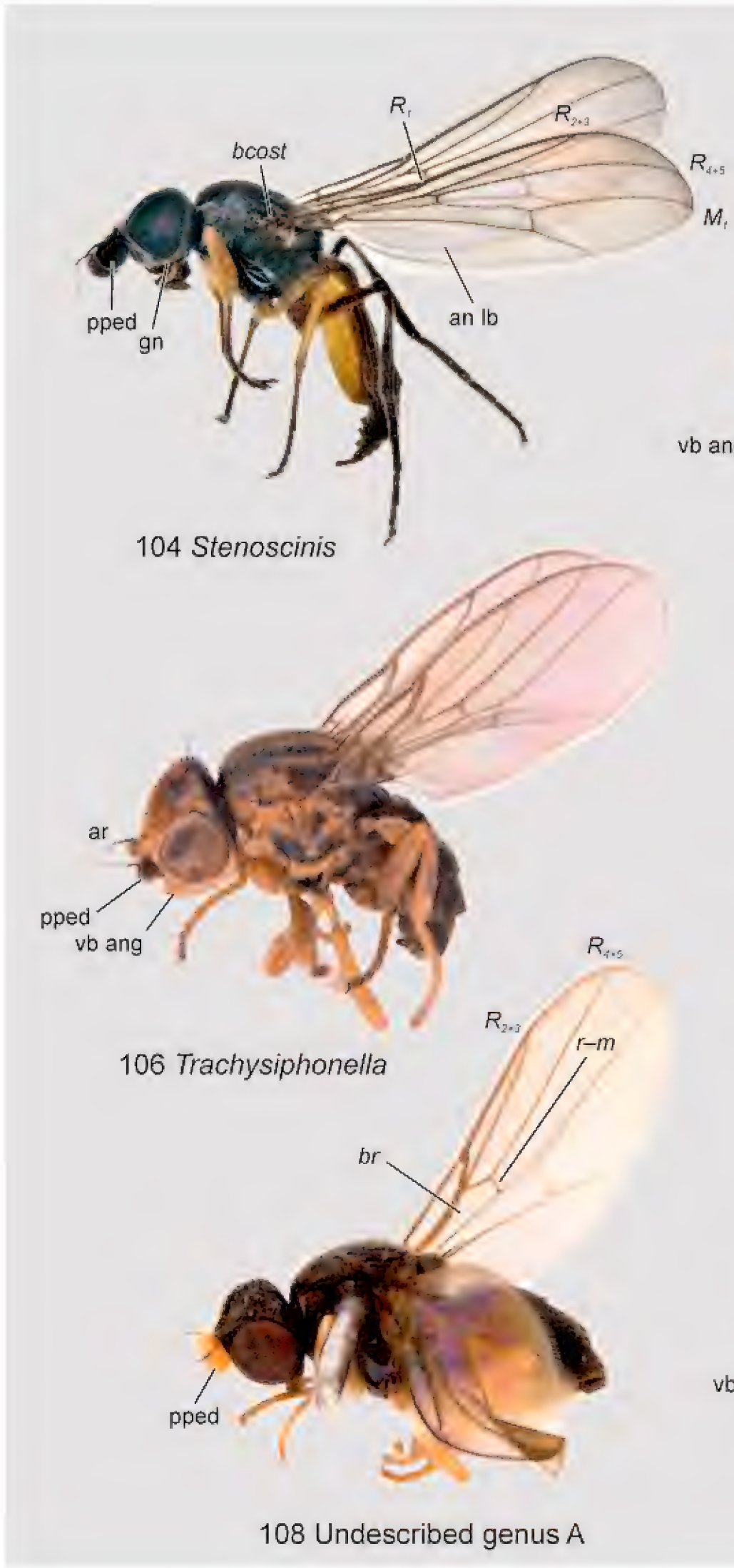
Tef is a cereal crop native to the Horn of Africa in Eritrea and Ethiopia, where it is an important human food. It is also cultivated to a lesser extent in Djibouti, Kenya, Somalia, Tanzania, Uganda and in the Arabian Peninsula. It is further marketed as a novel food and is often included in gluten-free diets, so it is also an important food crop for humans and livestock in other regions of the world (Bultosa & Umeta 2013; Yami 2013). Chloropids causing "dead heart" in Tef in Ethiopia are *Oscinella* (*C.*) *nartshukiana* and *Oscinella* sp. near *dimidiofrit* Becker, 1913 (Nigus & Damte 2018). Damte (2013: 172) listed the following chloropid species as having been reared from Tef in Ethiopia and are all regarded as minor pests (original references provided): *Thaumatomyia secunda* (Becker, 1912) (Chichaybelu *et al*. 2001: 225); the shoot flies *Elachiptera simplicipes* Becker, 1910 and *Lasiochaeta vulgaris* (Adams, 1905) (as *Melanochaeta*) and *Oscinella* (*C.*) *nartshukiana* (Sileshi 1994, 1997); *O.* (*Paroscinella*) *acuticornis* Becker, 1912 (Sileshi 1997); and *Rhopalopterum* sp. as a shoot fly (Sileshi 1997). Damte (2013: 176) stated "The Chloropidae flies infest Tef starting from crop germination and dominate up to the three-leaf stage (but they occur in combination with Muscidae flies in the other crop stages), whereas the Muscidae flies [*Atherigona* species] occur starting from the three-leaf stage and dominate between the heading and maturity of the crop." Damte (2013: 188) also included seasonal variation, depending on planting date, soil aridity and local climate, as well as tests with insecticide and stated that further research was required. The species mentioned above also attack other cereal crops (Barley, Sorghum and Wheat) and grasses (*Digitaria* and *Eragrostis* species) (Damte 2013: 176; Sileshi 1997). It should be noted that *Thaumatomyia* species are predators of Hemiptera: Sternorrhyncha (aphids or root aphids (Pemphigidae)) (Nartshuk 2014) and *Elachiptera* and *Lasiochaeta* Corti species are regarded as secondary invaders.

Sorghum is a plant grown for human consumption in many Afrotropical countries. It is another crop that has had a revival, as it can be grown in more arid conditions than many other grain crops. Deeming (1972: 3) summarised the results of an extensive study conducted in Samaru, Nigeria of dipterous species attacking Sorghum. He also included all records of pest species on Sorghum that had been published, or which he had received for identifications or that he had determined from extensive

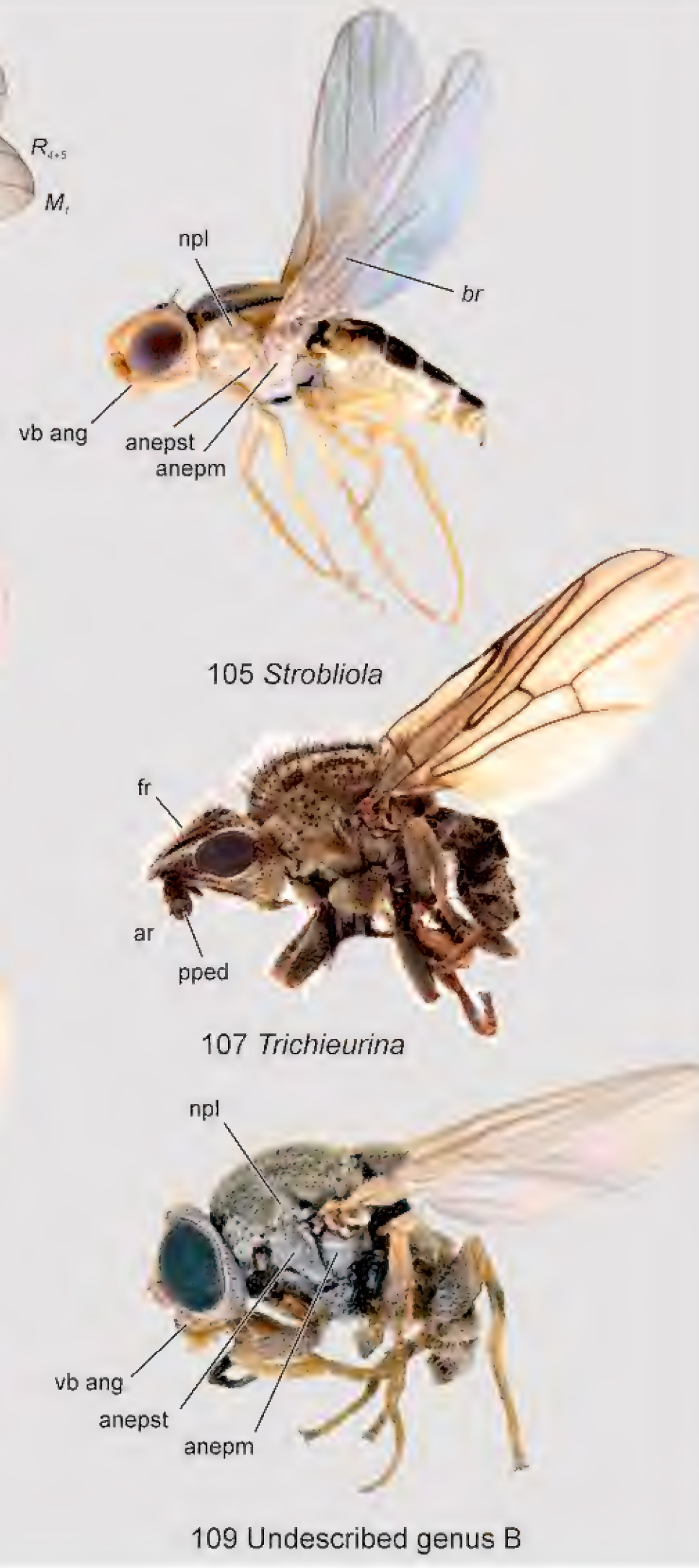


Figs 96.98–103. Habitus of Chloropidae (lateral views): (98) *Siphlus seminifer* Sabrosky; (99) *Siphonella oscinina* (Fallén) (non-Afrotropical); (100) *Speccafrons halophila* (Duda) (non-Afrotropical); (101) *Steleocerellus ensifer* (Thomson) (non-Afrotropical); (102) *Stenophthalmus ocellatus* Becker; (103) *Stenoscinis arnos* Malloch. Fig. 98 (© Trustees of Natural History Museum, London).

Abbreviations: an lb – anal lobe; ar – arista; *dm–m* – discal medial crossvein; gn – gena; oc tr – ocellar triangle; pped – postpedicel; prbs – proboscis; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; sct – scutum; sctl – scutellum; ts – tarsus.



104 *Stenoscinis*



105 *Strobliola*

106 *Trachysiphonella*

107 *Trichieurina*

108 Undescribed genus A

109 Undescribed genus B

Figs 96.104–109. Habitus of Chloropidae (lateral views): (104) *Stenoscinis* sp.; (105) *Strobliola flavofacies* (Becker); (106) *Trachysiphonella scutellata* (von Roser) (non-Afrotropical); (107) *Trichieurina pubescens* (Meigen) (non-Afrotropical); (108) Undescribed genus A; (109) Undescribed genus B.

Abbreviations: an lb – anal lobe; anepm – anepimeron; anepst – anepisternum; ar – arista; *bcost* – basicosta; *br* – basal radial cell; fr – frons; gn – gena; M_1 – first branch of media; npl – notopleuron; pped – postpedicel; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; vb ang – vibrissal angle.

studies of museum collections. Sorghum seedlings are damaged in the 3–4 leaf stage by *Oscinella* (*C.*) *nartshukiana* (as "*Oscinella* species c" *sensu* Deeming 1972: 7, 15) and by *Scoliophthalmus micantipennis*; these two chloropid species are primary invaders, especially during the early part of the rainy season, while they act as secondary invaders once *Atherigona soccata* Rondani (Muscidae) has damaged the plant. *Scoliophthalmus trapezoides* is usually a secondary invader and replaces *S. micantipennis* towards the end of the rainy season. "*Oscinella* species a" (*sensu* Deeming 1972: 14) and "*Oscinella* species b" (*sensu* Deeming 1972: 14), have both been reared from Sorghum, but "*Oscinella* species a" only in lower numbers in Nigeria, while "*Oscinella* species b" was recorded in Cameroon (Deeming 1972: 15). *Steleocerellus tenellus* was reared from Sorghum in Kenya. Other chloropid species have been reared from Sorghum and are included in Deeming (1972: 3), but these are thought to be secondary invaders. *Anatrichus erinaceus* has been recorded from South Africa as a shoot fly on Sorghum (Matthee & Oberholzer 1958), but it is not clear whether these are not secondary invaders. Deeming & Al-Dhafer (2012) recorded *Calamoncosis sorghivora* Deeming & Al-Dhafer, 2012 as being reared from damaged Sorghum stems in Yemen and it was noted that the species attacks Sorghum when under stress (either from too much or too little water). Deeming & Al-Dhafer (2012) also included records for species that could be primary or secondary invaders, these being: *Anacamptoneurum obliquum*, *Anatrichus pygmaeus*, *Steleocerellus tenellus* and *Strobliola flavofacies*. *Elachiptera occipitalis* has also been reared from Sorghum seedlings in Ethiopia (Deeming & Al-Dhafer 2012).

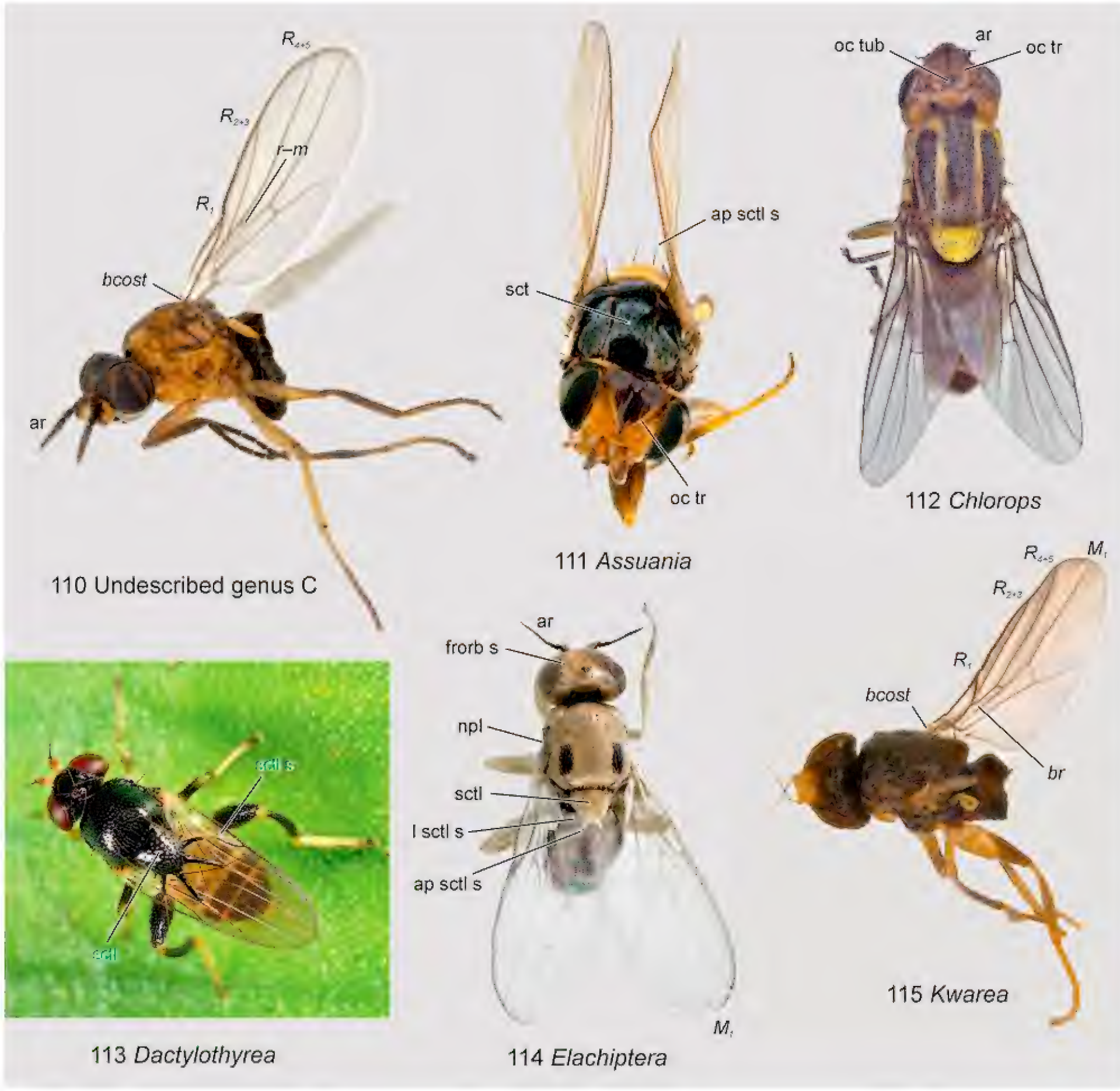
Maize, another important widespread crop grown in the Afrotropical Region, is also attacked by several Chloropidae species and further species have been reared from it, but it is not clear if these are primary or secondary invaders. *Scoliophthalmus micantipennis* and *S. trapezoides* are primary invaders, while it is not clear if *Anacamptoneurum obliquum*, *Stenophthalmus ocellatus* Becker, 1903 and *Strobliola flavofacies* are primary or secondary invaders. In the United States, Carmona *et al*. (2019) recorded the Wheat stem maggot (*Meromyza americana*) as an emerging pest of Maize when this is planted into a cover crop of Rye or Wheat without first killing-off the cover crop. Bereś (2015) discussed damage caused to Maize by the Frit fly, *Oscinella* (*O.*) *frit*, in Poland. There are 245 papers and monographs citing Frit fly as damaging Maize in Europe (M. von Tschirnhaus, pers. comm. 2021).

Sugarcane is grown commercially for sugar production in several Afrotropical countries. *Anacamptoneurum obliquum*, *Oscinella* (*C.*) *nartshukiana* and *Stenophthalmus ocellatus* have been reared from Sugarcane and could be primary invaders (Deeming 2003; Deeming & Al-Dhafer 2012). *Meromyza nigriventris* Macquart, 1835, a serious pest of various cereal crops, was recorded from Sugarcane in Iran, but further research is required to establish its pest status (Deeming 2003; Deeming & Al-Dhafer 2012); the same authors also recorded *Thaumatomyia glabra*, *T. notata* and *T. sulcifrons* (Becker, 1907), from Sugarcane and these may control root aphids of Sugarcane, as most species within this genus are predators of root aphids (Nikpay *et al*. 2017). *Mepachymerus sabroskyi* Kapoor, 1974 has been reared from the shoot-borer, *Chilo infuscatellus* (Snellen) (as *Chilotraea*) (Lepidoptera: Pyralidae) on Sugarcane in India (Kapoor 1974).

Many species in several Chloropidae genera, such as *Chlorops*, *Dicraeus*, *Meromyza* and *Oscinella*, are known to attack other cereal crops, including Barley, Oats, Rye (*Secale cereale* L.) and Wheat and an extensive literature exists on the subject. They also attack pasture grasses, causing considerable damage, as well as rushes (*Juncus* spp.) (Juncaceae), sedges and wild grasses. The following are, therefore, only examples of the major pest species and specialist agricultural literature should be consulted for additional in-depth information. *Oscinella* (*O.*) *frit* has been reared from Barley (to a lesser extent) and several pasture and wild grasses (Nartshuk & Andersson 2013: 128), Oats (Jonasson 2009) and Wheat (El-Wakeil *et al*. 2009), but appears to largely avoid Rye (Vickerman 1978). It is known to cause considerable damage in the young seedlings, often at the two- or five-leaf stage and seed heads at the milky grain stage, but can be controlled by pesticide treatments (El-Wakeil *et al*. 2009; Larsson 2009). It is currently unclear, however, how many species are involved in this species complex, as spring, summer and autumn forms appear different and molecular studies have not yet been undertaken. For further information on the potential species included, see Nartshuk & Andersson (2013: 125). It is of note that Nye (1958) mentioned differences in the distribution of spicules on larvae between *O.* (*O.*) *frit* populations usually reared from cultivated Oats and other grasses and those reared from *Anthoxanthum odoratum* L. and those reared from *Alopecurus pratensis* L. and *Arrhenatherum elatius* (L.) in Britain, while the adults all fall within the general limits of *O.* (*O.*) *frit*. Some closely related species in the Palaearctic Region may also be pests of cereal crops, namely: *O. nigerrima* (Macquart, 1835), *O. pusilla* (Meigen, 1830) and *O. vastator* (Curtis, 1845) (Nartshuk & Andersson 2013: 129). Deeming (2003), recorded *O.* (*C.*) *nartshukiana*, the most widespread *Oscinella* species in the Afrotropics, from the Arabian Peninsula, the Mediterranean area and Asia, as a major pest of various cereal crops and of pasture and wild grasses. Known host-plant associations of cereals and grasses of other Afrotropical *Oscinella* species were provided by Deeming (2003). Nielsen & Nielsen (1984) recorded *O.* (*O.*) *frit* and *O. pusilla* as major pests of pasture grasses in Denmark. Widespread *Oscinella* damage has also been observed on *Themeda* grass (a pasture grass) in KwaZulu-Natal, South Africa (Joubert 1985*a*, *b*). As far as it is known, larvae of all *Dicraeus* species develop within the seeds of grasses, including pasture grasses and some species can cause serious damage.

The Gout fly, *Chlorops pumilionis*, is a pest of Barley, Rye and Wheat and also damages the invasive weed Couch grass, *Elymus repens* (L.) Gould, in the Palaearctic (Kaniuczak 2009; Maneva *et al*. 2015) and *C. mugivorus* Nishijima & Kanmiya, 1975, is a pest of Barley, Oats, Rye and Wheat and also damages Couch grass in Japan (Nishijima & Kanmiya 1975). All other species of *Chlorops*, for which the biology is known, are primary invaders of grasses and sedges. The genus *Meromyza* is known from grasses, with two species known as pests of cereal crops: the Nearctic *M. americana*, which attacks Barley, Maize, Rye and Wheat (Kanmiya 1978) and is also known to develop in certain grasses (Carmona *et al*. 2019; Horber 1955); and the Holarctic, *M. nigriventris*, known as a pest of Barley, Oats, Rye and spring and winter Wheat (Nartshuk & Fedoseeva 2011). Two additional species have been reared from Wheat in the Palaearctic Region, although rarely:

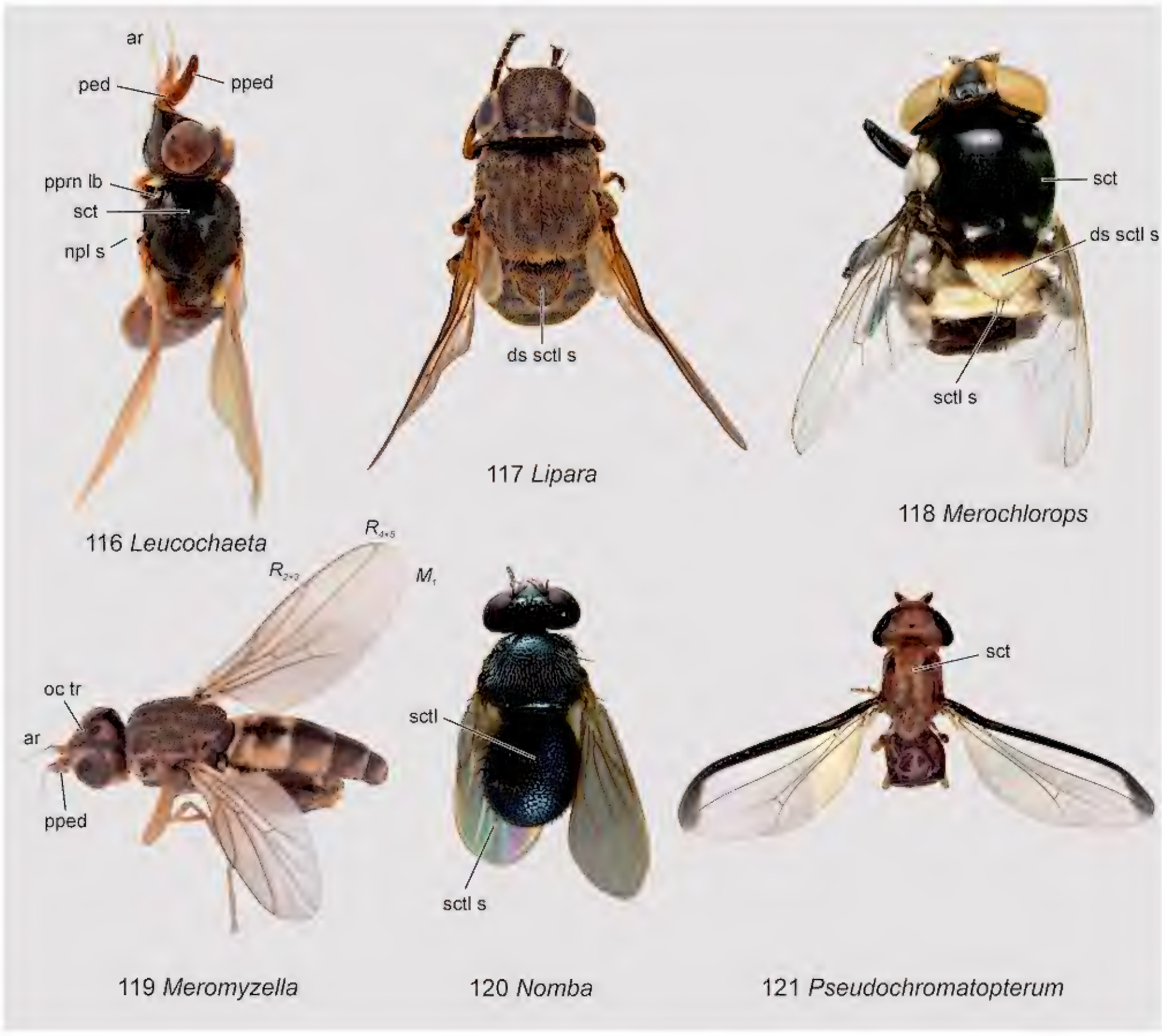
M. grandifemoris (Kanmiya, 1983) and *M. nigriseta* Fedoseeva, 1960 (Nartshuk & Fedoseeva 2011). Deeming (1981*b*) recorded *Camarota curvipennis* (Latreille, 1805), as a pest of Rye and also attacking Barley and Wheat in the Palaearctic Region, while Nartshuk & Andersson (2013: 155) listed this species as a pest of all these cereal crops and also of Oats in southern Europe and stated that larvae develop in shoots and ears.



Figs 96.110–115. Habitus of Chloropidae: (110) Undescribed genus C, lateral view; (111) *Assuania thalhammeri* (Strobl), antero-dorsal view (non-Afrotropical); (112) *Chlorops* sp., dorsal view (non-Afrotropical); (113) same, *Dactylothyrea* sp.; (114) same, *Elachiptera bimaculata* (Loew); (115) same, *Kwarea pallidihirta* Sabrosky. Fig. 113 (photograph © S.A. Marshall), Fig. 114 (photograph © National Museum of Wales).

Abbreviations: ap sctl s – apical scutellar seta; ar – arista; *bcost* – basicosta; *br* – basal radial cell; frorb s – fronto-orbital seta; l sctl s – lateral scutellar seta; M_1 – first branch of media; npl – notopleuron; oc tr – ocellar triangle; oc tub – ocellar tubercle; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; sct – scutum; sctl – scutellum; sctl s – scutellar seta.

Additional plant pests include, *Elachiptera megaspis*, a stem-miner of Watercress (Ismay 1978). Gladioli are attacked by *Epimadiza hirta*, with larvae destroying the young shoots, preventing flowering (Ferrar 1987: 111; Sabrosky 1947). It is a serious pest of gladioli in the Afrotropics and has been recorded from Kenya, Uganda and Zimbabwe (Cuthbertson 1935; Gachukia *et al*. 2005). Ferrar (1987: 117) reported that seedlings of the Kapok tree are attacked by *Ep. delattrei* Séguy, 1953, causing economic damage. In India, an unidentified *Thressa* species has been reared from Ginger, while *Merochlorops dimorphus* has been repeatedly reared from the weed Ginger lily, *Hedychium gardnerianum* and has been investigated as a potential biocontrol agent (Djeddour *et al*. 2011); it is unclear if several *Merochlorops* Howlett species are involved, as a paper by Gupta *et al*. (2019) described two parasites on potential biocontrol agents in the *Merochlorops* complex. *Neoloxotaenia gracilis* has also been reared from Ginger lily, *Hedychium gardnerianum* (Djeddour *et al*. 2011) and shoots and rhizomes of Ginger and the spice

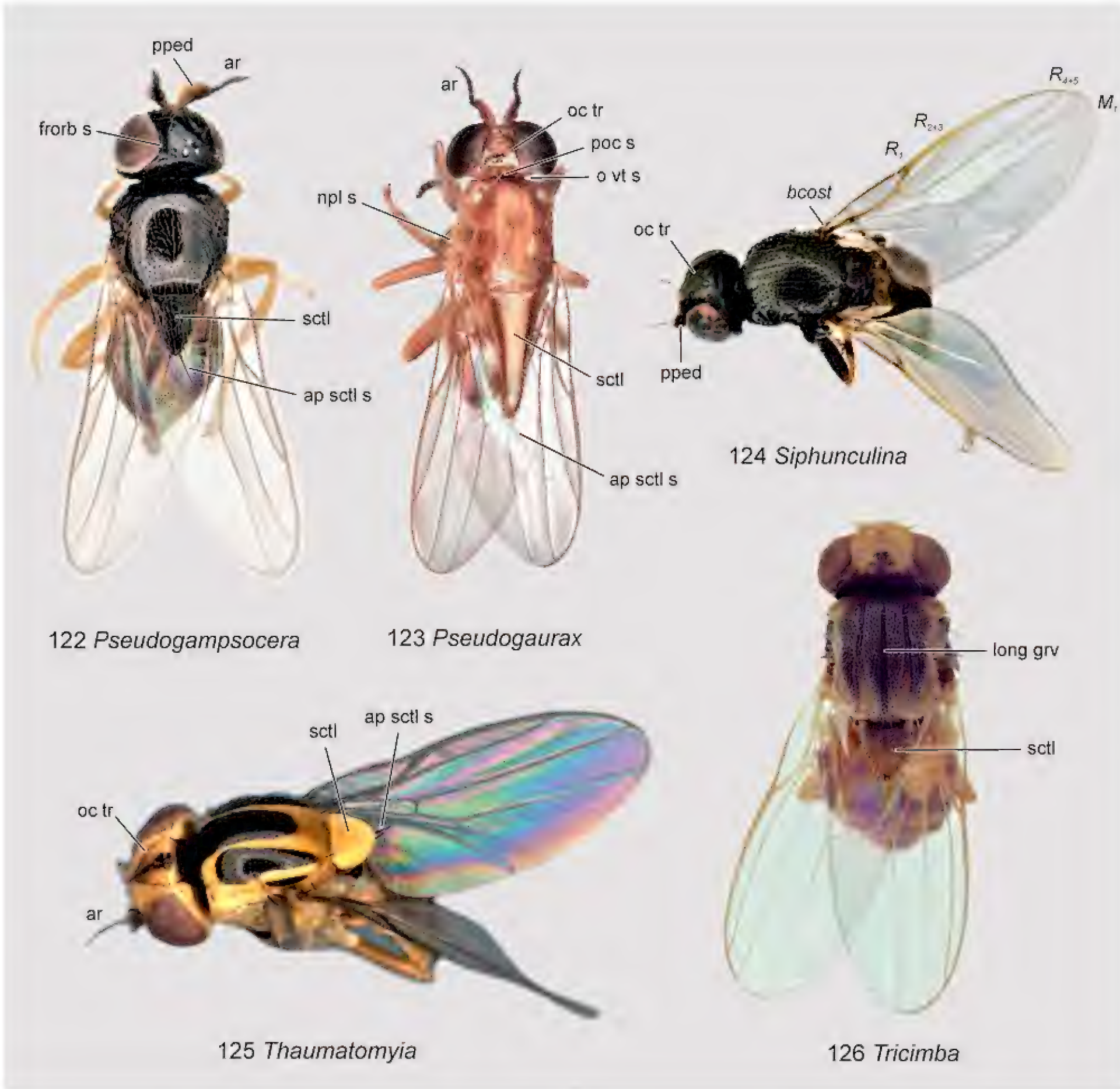


Figs 96.116–121. Habitus of Chloropidae (dorsal views): (116) *Leucochaeta trapezina* Becker, dorsal view; (117) *Lipara lucens* Meigen (non-Afrotropical); (118) *Merochlorops ceylonica* (Duda); (119) *Meromyzella capensis* (Loew); (120) *Nomba* sp.; (121) *Pseudochromatopterum rileyi* Deeming. Fig. 116 (courtesy Y. Ang), Fig. 118 (© National Museum of Wales), Fig. 121 (© Trustees of Natural History Museum, London).

Abbreviations: ar – arista; ds sctl s – discal scutellar setulae; M_1 – first branch of media; npl s – notopleural seta; oc tr – ocellar triangle; ped – pedicel; pped – postpedicel; pprn lb – postpronotal lobe; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; sct – scutum; sctl – scutellum; sctl s – scutellar seta.

Cardamom are severely damaged by the shoot fly *M. flavipes* (Malloch, 1927) (Nartshuk *et al*. 2015). A rearing of *N. gracilis* from Cardamom is also included in Deeming & Al-Dhafer (2012) and J.C. Deeming (pers. obs.) reported *Cordylosomides valparainus* (Duda, 1936) as being reared from Cardamom.

Chloropidae are not just pests and vectors, they also deliver important ecosystem services. Many chloropid species are saprophagous and, as such, are important in the decomposition of vegetable matter. In the Northern Hemisphere, many Chloropidae species occur in grasslands and wetlands, where some

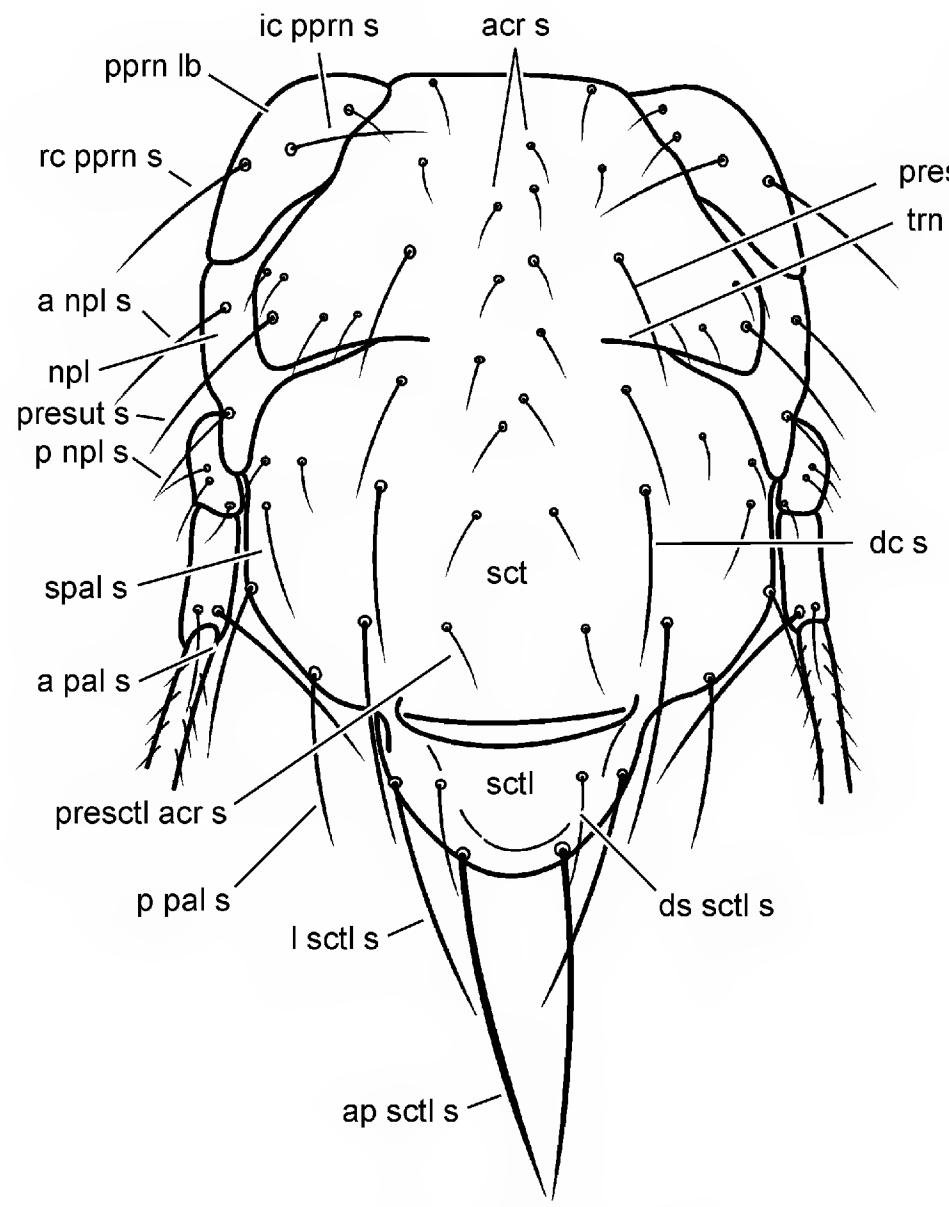


Figs 96.122–126. Habitus of Chloropidae (dorsal views): (122) *Pseudogampsocera scutellata* (Lamb); (123) *Pseudogaurax sicarius* (Lamb); (124) *Siphunculina aenea* (Macquart); (125) *Thaumatomyia notata* (Meigen); (126) *Tricimba* sp. Fig. 123 (© Trustees of Natural History Museum, London).

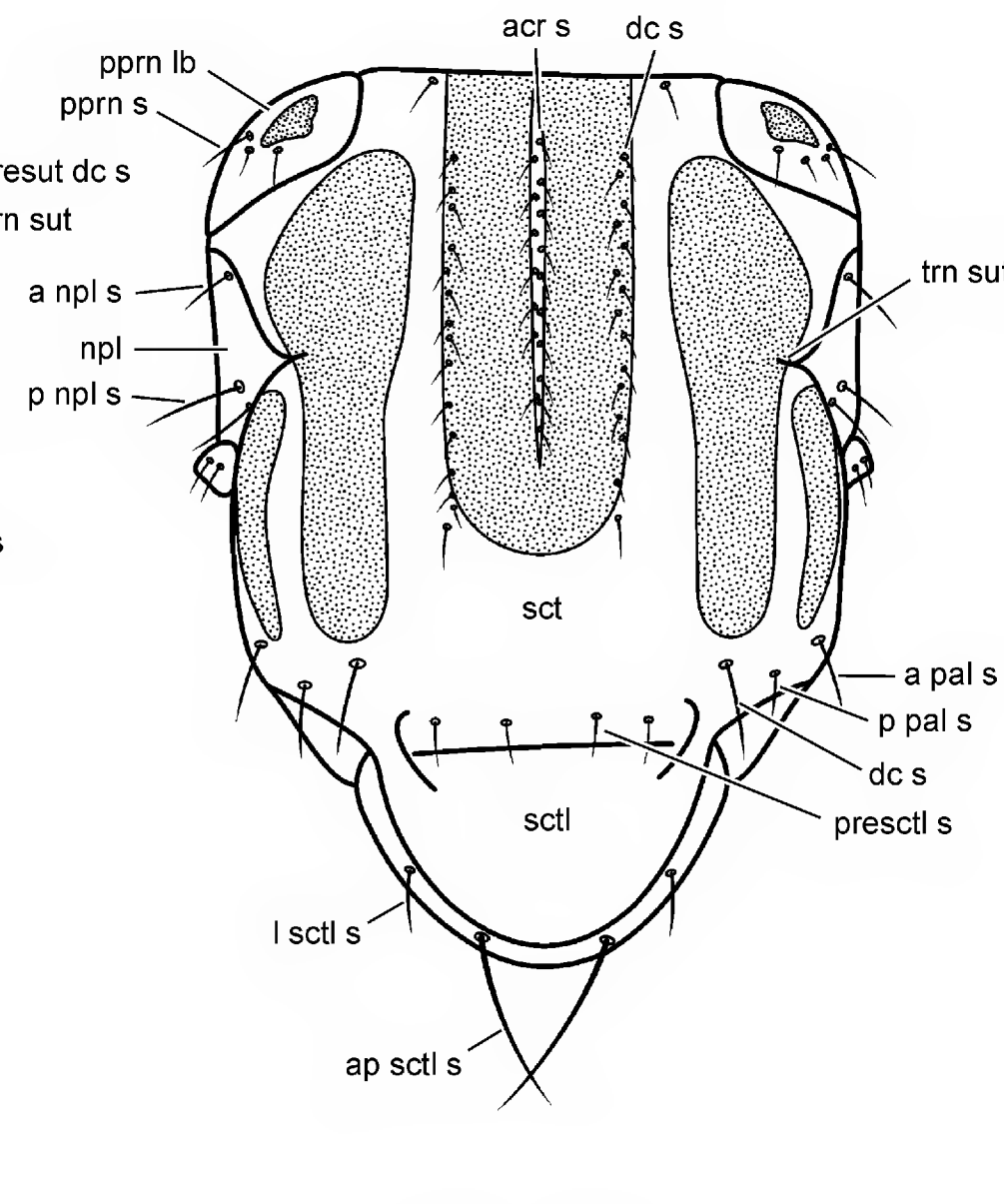
Abbreviations: ap sctl s – apical scutellar seta; ar – arista; *bcost* – basicosta; frorb s – fronto-orbital seta; long grv – longitudinal groove; M_1 – first branch of media; npl s – notopleural seta; o vt s – outer vertical seta; oc tr – ocellar triangle; poc s – post-ocellar seta; pped – postpedicel; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; sctl – scutellum.

have rather specific micro-habitat requirements, thus making them useful in assessing sites within these habitats for conservation purposes. Chloropidae act as control agents for other plants and animals. In the Afrotropics, larvae of *Pseudogaurax* are known to be predators of egg masses of spiders and mantid oothecae (Boulard *et al*. 1989; Cogan 1977). The larvae of extralimital species are known to also be predacious upon the egg masses of ants (Hymenoptera: Formicidae), Megaloptera and Orthoptera and to parasitise Lepidoptera larvae and pupae (Ismay & Ang 2019) and to develop in the egg masses of Amplypygi (Corey & Hebets 2017; Gillung & Borkent 2017; Viquez & De Armas 2009). Two other genera of grasshopper egg parasites, namely: *Dysartia* Sabrosky and *Olcella* (non-Afrotropical), were discovered during a study of integrated pest management of grasshopper pest species in North America (Dysart 1991, 2020; Sabrosky 1991). In the Nearctic Region, *Pseudogaurax signatus* is a major biocontrol agent of the venomous Black widow spider, *Lactrodectus* Walckenaer (Theridiidae), as larvae develop in its egg-sacs. Between 6–40% of egg-sacs are infested, resulting in *ca* 90% egg mortality (Gillung & Borkent 2017). Gillung & Borkent (2017) published an excellent review of Diptera species utilising spiders and in addition to *Pseudogaurax* they further list *Conioscinella*, *Gaurax*, *Oscinella*, *Oscinisoma* Lioy (non-Afrotropical), *Siphonella* and *Tricimba*, as predators, parasites or kleptoparasites of arachnids (Tschirnhaus *et al*. 2015). *Lipara* species damage Common reed and add to its control where this plant is considered undesirable and *Platycephala planifrons* has been investigated as a potential control agent of reeds in North America (Häfliger *et al*. 2005).

Chloropidae are frequently recorded as flower visitors, but their role in pollination is largely unknown. Many pollination studies omit them, due to their small size and the lack of modern identification keys for most regions. Chloropidae are known to pollinate certain plants, however, in particular Orchidaceae and other plants with specialised pollination strategies, e.g., trap flowers. Larson *et al*. (2001), noted that Chloropidae species could be important pollinators, in



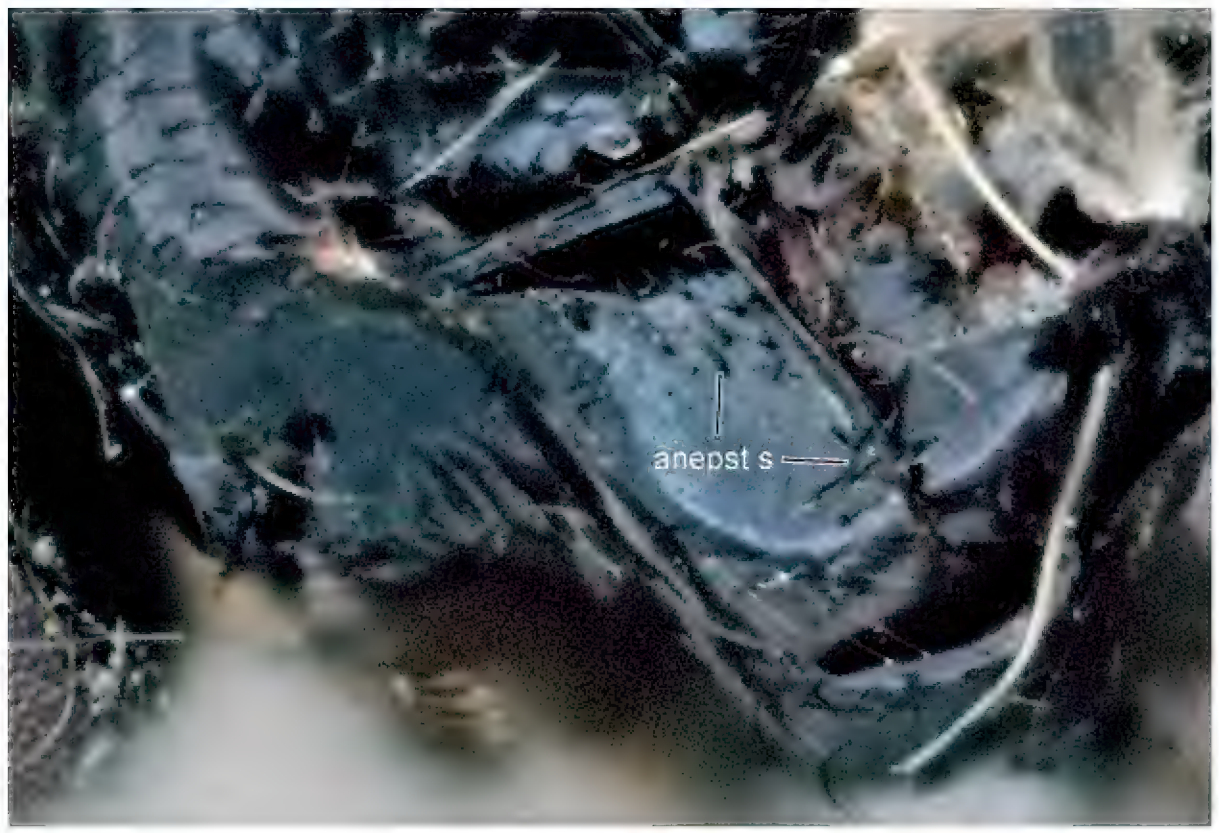
127 *Apotropina*



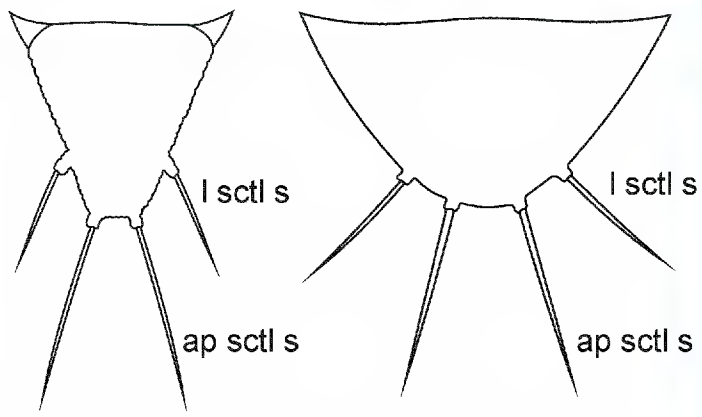
128 *Lasiosina*

Figs 96.127–128. Thoraces of Chloropidae (dorsal views; non-Afrotropical): (127) *Apotropina longepilosa* (Strobl); (128) *Lasiosina* sp. Figs 127, 128 (Andersson 1977, 10A, 10B).

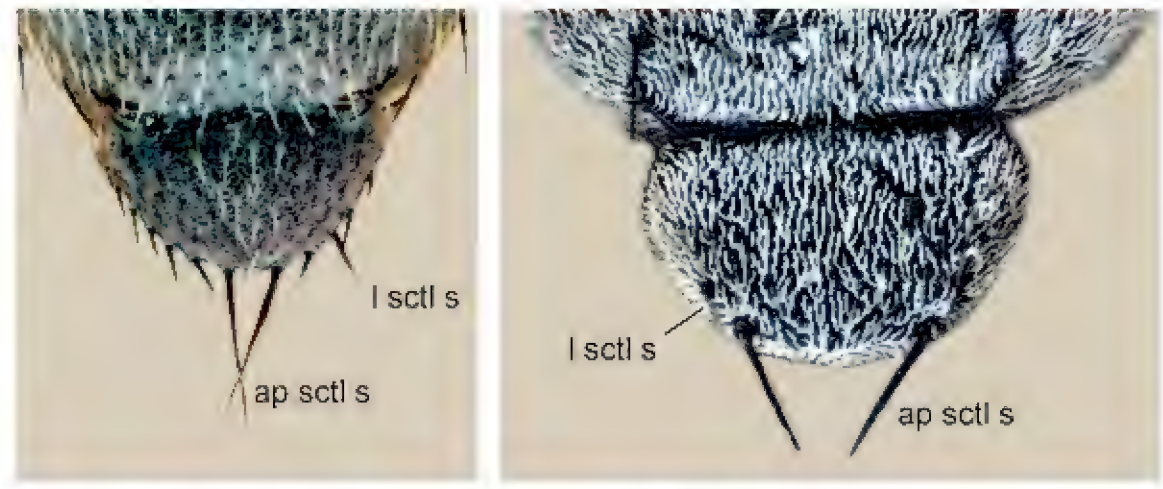
Abbreviations: a npl s – anterior notopleural seta; a pal s – anterior postalar seta; acr s – acrostichal setae; ap sctl s – apical scutellar seta; dc s – dorsocentral seta; ds sctl s – discal scutellar seta; ic pprn s – inclinate postpronotal seta; l sctl s – lateral scutellar seta; npl – notopleuron; p npl s – posterior notopleural seta; p pal s – posterior postalar seta; pprn lb – postpronotal lobe; pprn s – postpronotal seta; presctl acr s – prescutellar acrostichal seta; presctl s – prescutellar seta; presut dc s – presutural dorsocentral seta; presut s – presutural seta; rc pprn s – reclinate postpronotal seta; sct – scutum; sctl – scutellum; spal s – supra-alar seta; trn sut – transverse suture.



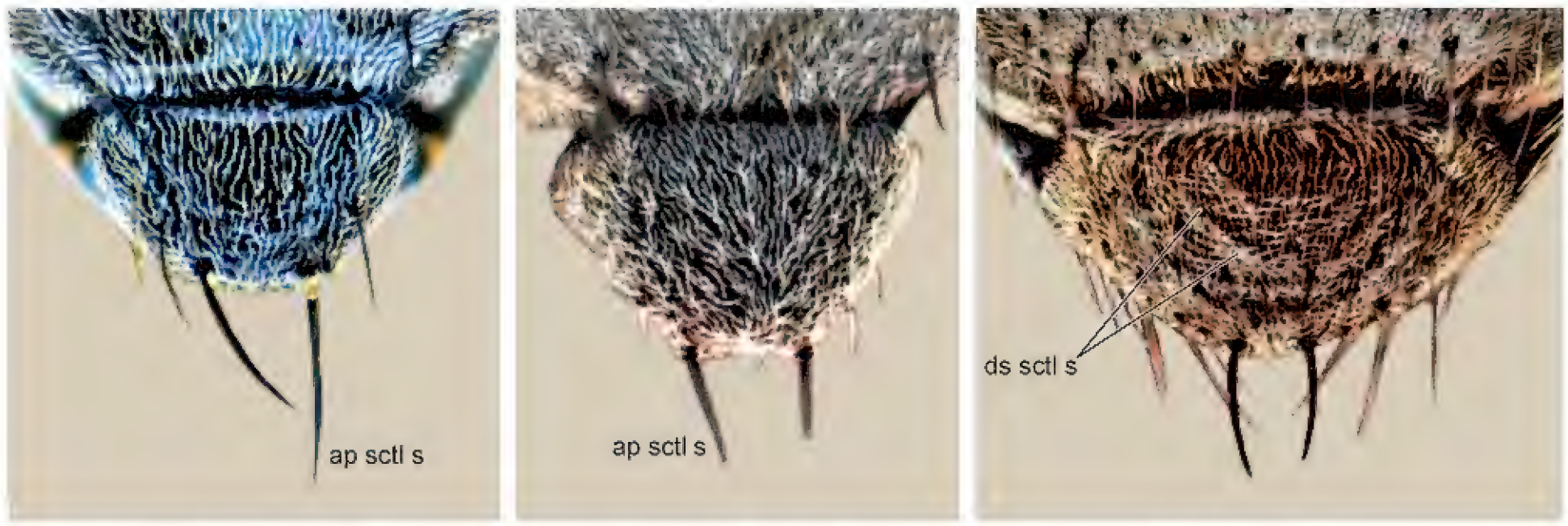
129 *Rhodesiella*



130 *Cadrema*



131 *Rhodesiella* 132 *Rhodesiella* 133 *Anacamptoneurum* 134 *Aphanotrigonum*

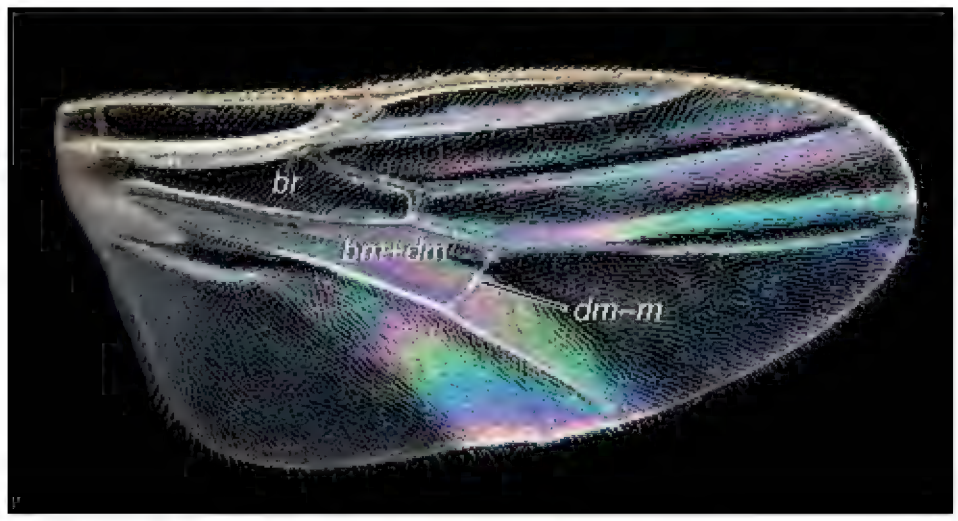


135 *Lasiochaeta* 136 *Meijerella* 137 *Speccafrons*

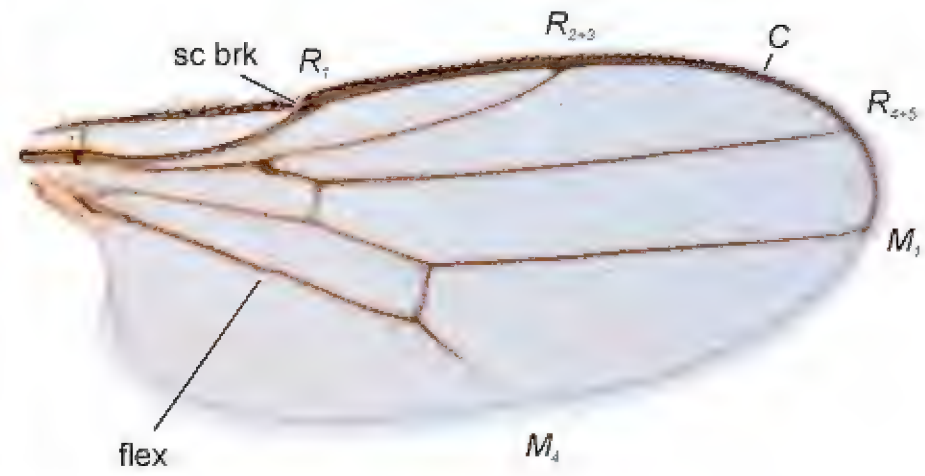
Figs 96.129–137. Thoracic features and scutella of Chloropidae: (129) anepisternum of *Rhodesiella* sp., lateral view; (130) katepisternum of *Cadrema pallida* (Loew), lateral view; (131) scutellum of *R. formosa* (Lamb), dorsal view; (132) same, *R. infumata* (Becker); (133) same, *Anacamptoneurum obliquum* Becker; (134) same, *Aphanotrigonum femorellum* Collin; (135) same, *Lasiochaeta atricornis* (Adams); (136) same, *Meijerella inaequalis* (Becker); (137) same, *Speccafrons halophila* (Duda) (non-Afrotropical).

Abbreviations: anepst s – anepisternal setulae; ap sctl s – apical scutellar seta; ds sctl s – discal scutellar setulae; kepst s – katepisternal seta; l sctl s – lateral scutellar seta.

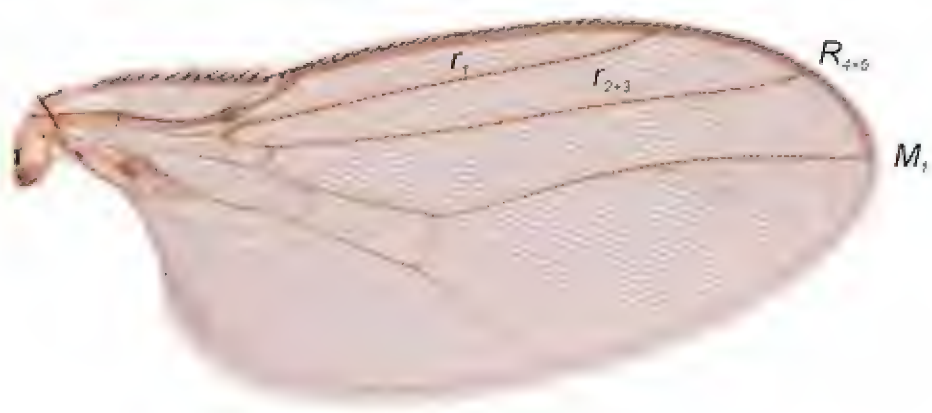
particular, of specialised flowers such as in the non-Afrotropical orchid species, *Herminium monarchis* (L.) R. Br. (Nilsson 1979) and *Peltandra virginica* (L.) Schott (Patt *et al*. 1989) (both Orchidaceae). Several *Genoplesium* species (Orchidaceae) are pollinated by Chloropidae, including the critically endangered Tuncurry midge orchid, *G. littorale* D.L. Jones, which is pollinated by five putative chloropid species in two genera, *Cadrema* and *Conioscinella* (Bower *et al*. 2015). Oelschlägel *et al*. (2015) demonstrated that *Aristolochia rotunda* L. (Aristolochiaceae) is pollinated by females of the kleptoparasitic chloropid species *Trachysiphonella ruficeps* (Macquart, 1835); the plant "cheats" on the flies, by emitting a scent that mimics freshly crushed Miridae bugs, the fluids from which would be the normal food of the flies. The attracted flies are trapped by the trap flower and it was observed that *T. ruficeps* transport pollen from the male stage to the female stage of the flower. Other species of *Aristolochia* are visited by Chloropidae, but their pollination systems require further investigating (Oelschlägel *et al*. 2014, 2016). *Aristolochia arcuata* Mast. and *Ceropegia* (Apocynaceae) are pollinated by chloropids (Berjano *et al*. 2009; Heiduk *et al*.



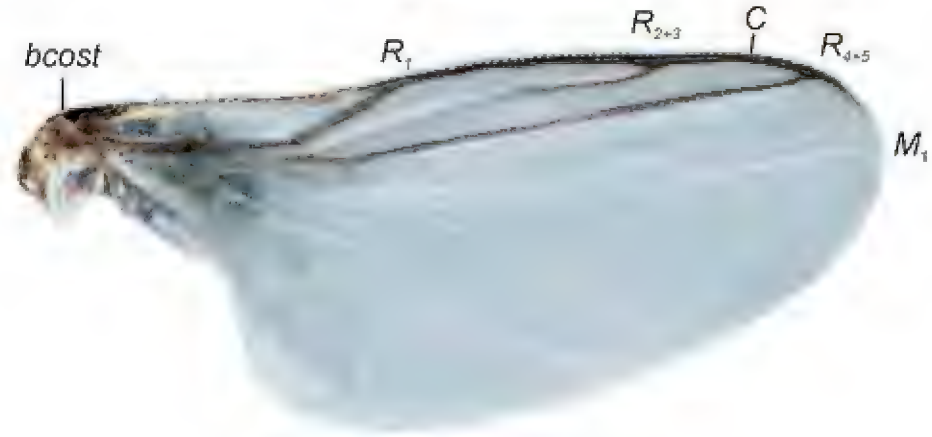
138 *Anacamptoneurum*



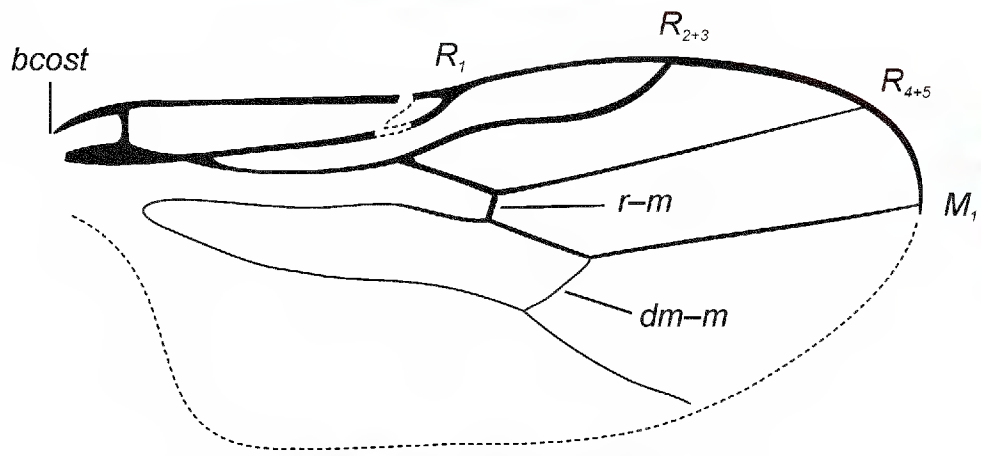
139 *Apotropina*



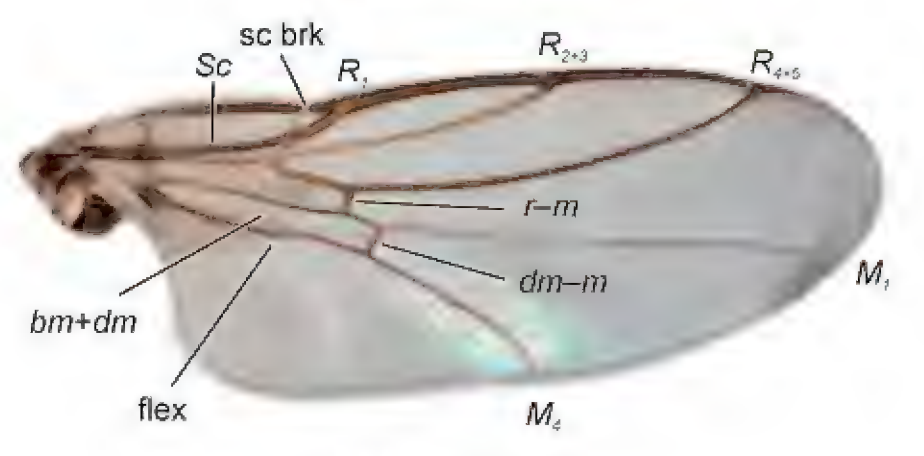
140 *Arcuator*



141 *Calamoncosis*



142 *Camptoscinella*



143 *Diplotoxa* (*Diplotoxa*)

Figs 96.138–143. Wings of Chloropidae (dorsal views): (138) *Anacamptoneurum obliquum* Becker; (139) *Apotropina* sp.; (140) *Arcuator stigmaticus* (Lamb); (141) *Calamoncosis abbreviata* Deeming (non-Afrotropical); (142) *Camptoscinella annulitibia* Sabrosky; (143) *Diplotoxa* (*Diplotoxa*) *messoria* (Fallén) (non-Afrotropical). Fig. 141 (© National Museum of Wales), Fig. 142 (after Sabrosky 1951, fig. 18), Fig. 143 (courtesy Y. Ang).

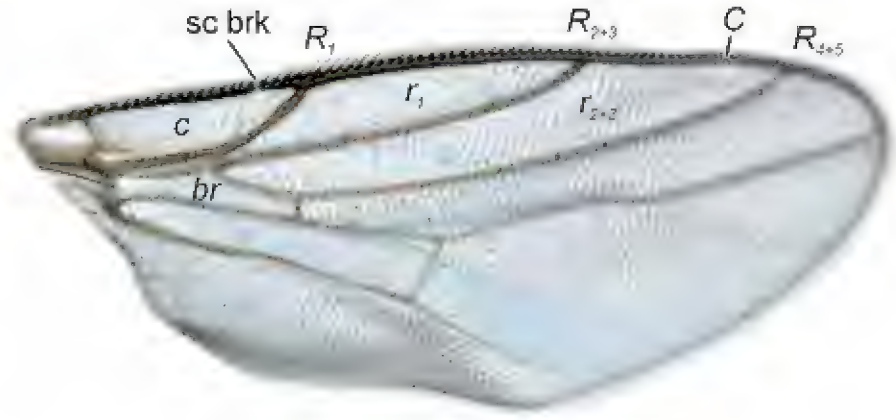
Abbreviations: *bcost* – basicosta; *bm+dm* – basal medial cell + discal medial cell; *br* – basal radial cell; *C* – costal vein; *dm–m* – discal medial crossvein; flex – flexure; M_1 – first branch of media; M_4 – fourth branch of media; r_1 – first radial cell; R_1 – anterior branch of radius; r_{2+3} – second + third radial cell; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Sc* – subcostal vein; sc brk – subcostal break.

2015*a*, *b*, 2016, 2017; Ollerton *et al*. 2009) and *Pleurothallis* orchids (Orchidaceae), which apparently emits a fish odour, are pollinated by species of *Tricimba* (Borba & Semir 2001). Wiesenborn (2016), studied the pollination of *Phoradendron coryae* Trel. (Santalaceae), a mistletoe on oak trees (*Quercus* sp.) (Fagaceae) and recorded chloropid flies in four genera: *Conioscinella*, *Hippelates*, *Liohippelates* and *Olcella* (non-Afrotropical), with *Liohippelates* being the dominant pollinator, as it was most often encountered and carried the largest pollen load.

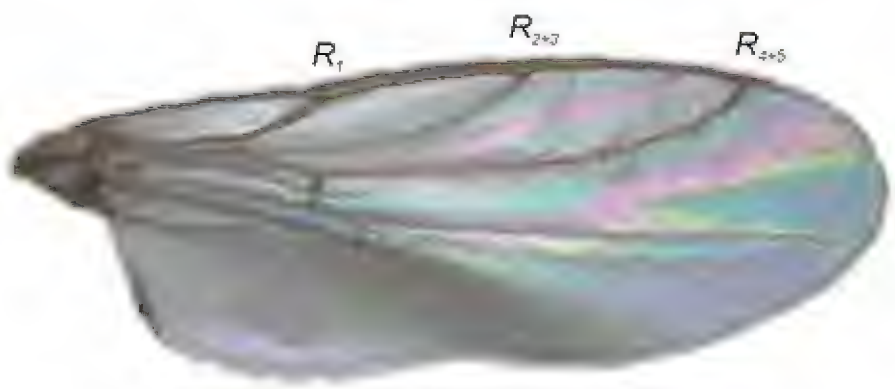
Classification

The Chloropidae is clearly defined as a monophyletic group (Nartshuk & Andersson 2013: 49; Riccardi & Amorim 2020). The family is currently assigned to the superfamily Carnoidea, as sister-group to the Milichiidae (Woodley *et al*. 2009: 91) and Bayless (2016) and Wiegmann *et al*. (2011) confirmed the close relationship with Milichiidae, but these two papers and a more recent paper (Bayless *et al*. 2021), despite including molecular techniques, have also not resolved the superfamily placement of the Chloropidae. The phylogenetic classification within the Chloropidae remains unclear, however, and different opinions have been expressed in the literature, which were summarised and elaborated on in Andersson (1977), Nartshuk & Andersson (2013: 49) and Riccardi & Amorim (2020). Further studies, incorporating both morphological and molecular characters, are required, that include examples of all genera from all subfamilies that occur globally.

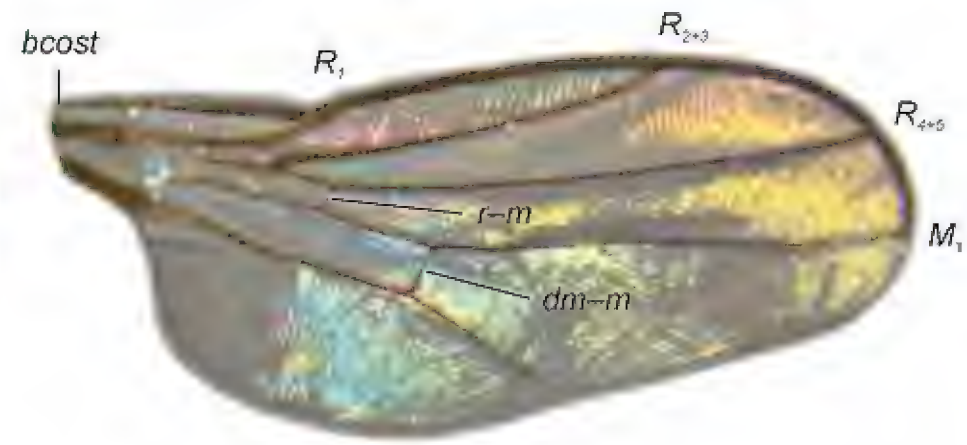
144 *Eribolus*



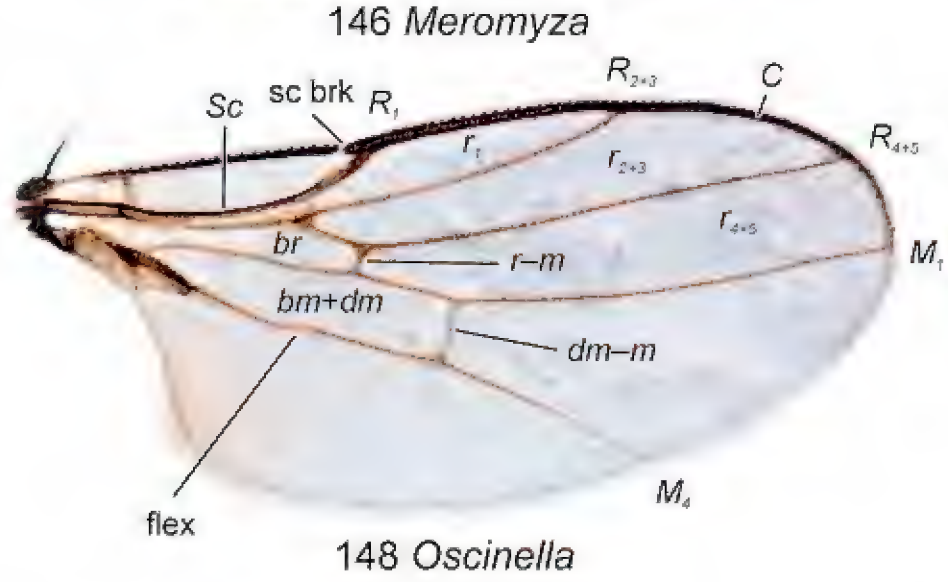
145 *Gaurax*



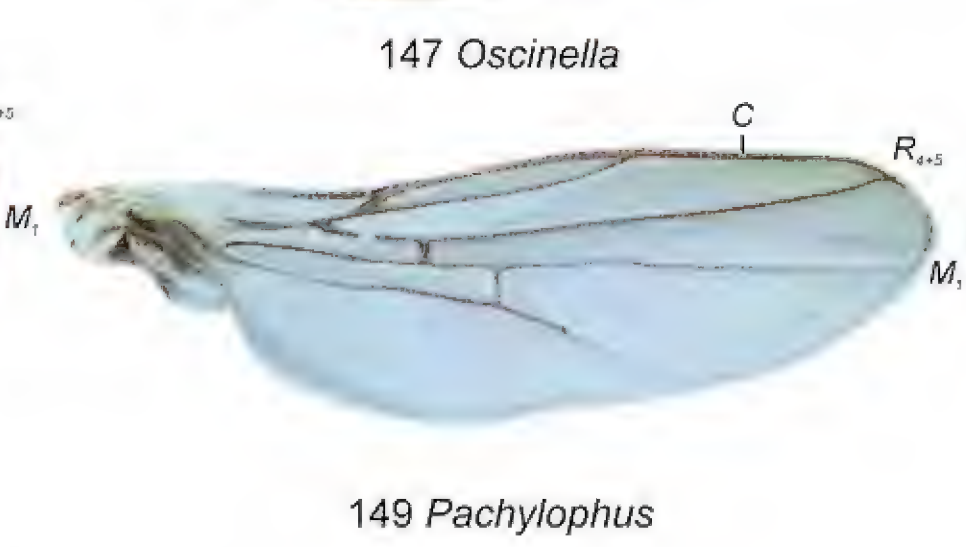
146 *Meromyza*



147 *Oscinella*



148 *Oscinella*



149 *Pachylophus*

Figs 96.144–149. Wings of Chloropidae (dorsal views): (144) *Eribolus* sp.; (145) *Gaurax fascipes* Becker (non-Afrotropical); (146) *Meromyza saltatrix* (L.) (non-Afrotropical); (147) *Oscinella* sp.; (148) *O*. (*O.*) *frit* (L.) (non-Afrotropical); (149) *Pachylophus gallagheri* Deeming. Fig. 146 (© Trustees of Natural History Museum, London), Fig. 149 (© National Museum of Wales).

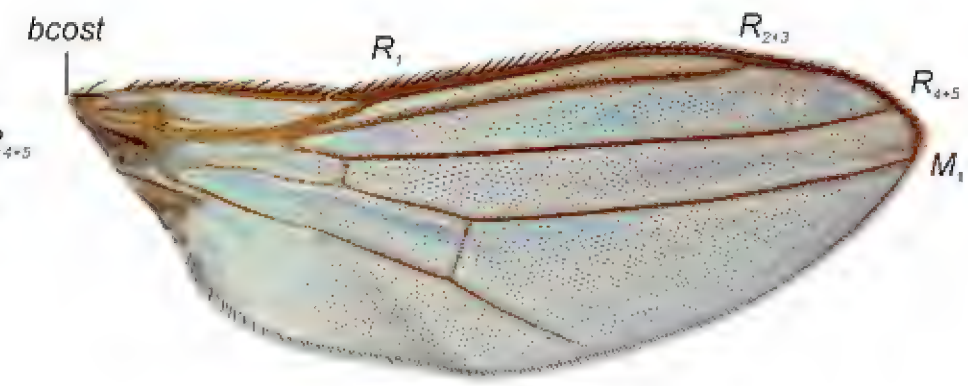
Abbreviations: *bcost* – basicosta; *bm+dm* – basal medial cell + discal medial cell; *br* – basal radial cell; *c* – costal cell; *C* – costal vein; *dm–m* – discal medial crossvein; flex – flexure; M_1 – first branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; r_1 – first radial cell; r_{2+3} – second + third radial cell; R_{2+3} – second branch of radius; r_{4+5} – fourth + fifth radial cells; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Sc* – subcostal vein; sc brk – subcostal break.

The subfamily classification is less clear, with either three or four subfamilies recognised. Sabrosky (1987: 1050) and Wheeler (2010: 1138), recognised three subfamilies, Chloropinae, Oscinellinae and Siphonellopsinae, while Cherian (2002: 44), Nartshuk (2012), Nartshuk & Andersson (2013: 51) and Riccardi & Amorim (2020), separated Rhodesiellinae from the Oscinellinae. Nartshuk (2012) retained the Rhodesiellinae in a world checklist of the genera of Chloropidae. Riccardi & Amorim (2020), however, pointed out that the genera included in Rhodesiellinae may correspond to an early branching group of genera at the base of the Oscinellinae, in a study on the genera of Oscinellinae (Bazyar 2019) and that the Rhodesiellinae is poorly defined. The separation of Rhodesiellinae from Oscinellinae depends largely on the former having proclinate ocellar setae, but *Stenoscinis* and some other genera do not fit well in Rhodesiellinae and this problem needs to be considered in a wider perspective. Until this work is complete the three traditional subfamilies are here retained.

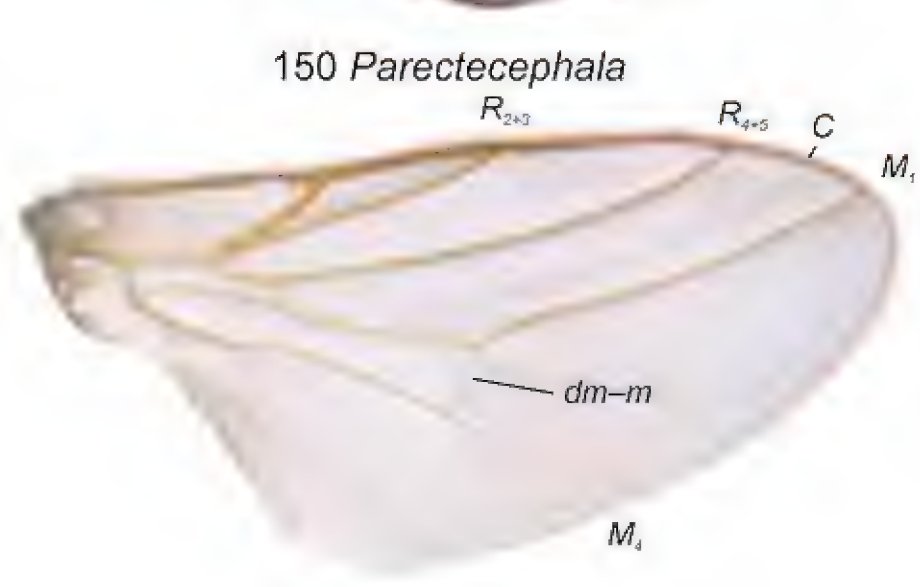
Chloropinae are perhaps better understood than the Oscinellinae and most species within this subfamily have the costal wing vein (C) extended to vein R_{4+5}, but this may be extended one-quarter distance to vein M_1 (e.g., Figs 150, 153) and the ocellar setae, if developed, are proclinate. An excellent study of their phylogeny was conducted recently by Riccardi & Amorim (2020). There are still numerous undescribed species, however, and difficulties with some generic concepts. Until further studies are completed, the following concepts are retained. In agreement with Spencer (1986), Wheeler (2010: 1149) and Wheeler & Forrest (2003), *Elliponeura* and *Pseudopachychaeta* are here treated as subgenera of *Diplotoxa*, along with *Diplotoxa sensu stricto*. Riccardi & Amorim (2020) retained these as separate genera, but pointed out that further work is required to establish their generic limits.

Oscinellinae is the largest subfamily in the Afrotropical Region and globally. Wing vein R_{4+5} nearly always reaches vein M_1 and the ocellar setae are usually erect or reclinate. Several segregates within the Oscinellinae appear to represent undescribed genera and these have been included in the key as "Undescribed genus A", *etc*. There are more undescribed species of Oscinellinae than in the other two subfamilies combined and some generic concepts in the Oscinellinae are unsatisfactory and require much additional work. While some problems have been resolved by the description of new genera, such as *Arcuator* (Sabrosky 1985), the limits of many genera (e.g., *Conioscinella*) remain unclear. Until further studies are completed, the following concepts are retained. Cherian (2012) sank *Fiebrigella*, now *Lasiambia* and *Polyodaspis* as junior synonyms of *Anacamptoneurum* Becker, but Bazyar *et al*. (2015), Nartshuk (2016) and Nartshuk *et al*. (2020) treated these as separate genera. In concurrence with Bazyar *et al*. and Nartshuk, these are here retained as separate genera. After publication of the identification key to brachypterous flies

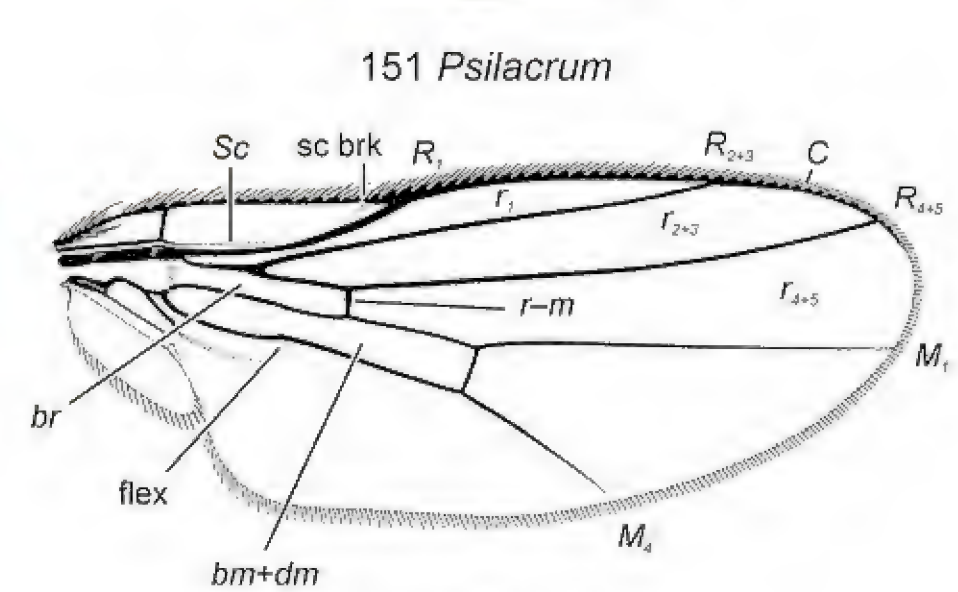
150 *Parectecephala*



151 *Psilacrum*



152 *Rhodesiella*



153 *Chlorops*

Figs 96.150–153. Wings of Chloropidae (dorsal views): (150) *Parectecephala gigas* Sabrosky; (151) *Psilacrum* sp.; (152) *Rhodesiella* sp.; (153) *Chlorops certimus* Adams (non-Afrotropical). Fig. 153 (after Sabrosky 1987, fig. 40).

Abbreviations: *bcost* – basicosta; *bm+dm* – basal medial cell + discal medial cell; *br* – basal radial cell; *C* – costal vein; *dm–m* – discal medial crossvein; flex – flexure; M_1 – first branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; r_1 – first radial cell; r_{2+3} – second + third radial cell; R_{2+3} – second branch of radius; r_{4+5} – fourth + fifth radial cells; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Sc* – subcostal vein; sc brk – subcostal break.

by Marshall *et al*. (2017: 353), Mlynarek & Wheeler (2018) synonymised the mainly Oriental genus *Myrmecosepsis* under *Anatrichus* and this is followed here. They also synonymised the former genus *Cyrtomomyia* Becker under *Elachiptera*, but all literature is still under *Cyrtomomyia*. There is considerable confusion over the limits and correct name of *Fiebrigella* as Tschirnhaus (1992) stated that the type species of *Fiebrigella*, *F. verrucosa* Duda, 1921 is not congeneric with the Palaearctic species placed within that genus. He therefore transferred the Palaearctic species to *Lasiambia*; since then, the species from the Palaearctic Region (Nartshuk 2012 and 2015) and from the Afrotropical Region (Deeming 2011; Dawah *et al*. 2020) have been interpreted as *Lasiambia*, while the species from the Neotropical Region (Wheeler 2010) have been retained in *Fiebrigella*. The checklist of Chloropidae genera (Nartshuk 2012) retained the Oriental species in *Fiebrigella*. *Lasiambia* is here applied for all Afrotropical species until the matter is resolved. The name *Hippelates* has been applied in the Old World for species with a strong anteroventral tibial spur, but these species have now been removed to other genera (*Arcuator* and *Cadrema*), that are not closely related to *Hippelates*. In the New World species have been removed to several genera including the closely related *Liohippelates*, a genus that is also of economic importance, however, further work is still required to resolve relationships within this grouping. There is currently confusion over generic limits with *Incertella* and *Microcercis* and it is not possible to accurately determine how many species should be included in both; these and two other genera require additional study to clarify the generic placements (Nartshuk & Przhiboro 2009). Deeming & Al-Dhafer (2012) is followed here, as treating *Incertella* as included in *Microcercis*, a genus proposed some few months earlier. The genus *Oscinella* includes several subgenera of which *O*. (*Cyclocercula*), *O*. (*Paroscinella*) and *Oscinella sensu stricto* occur in the Afrotropical Region. Many species of the genus have not been assigned to subgenera and future examination of types may reveal that some do not belong to *Oscinella*. Following Wheeler (2010: 1138) *Rhodesiella* is here retained within the subfamily Oscinellinae and in agreement with Nartshuk (2012) this genus is included in the tribe Rhodesiellini.

Siphonellopsinae is the smallest subfamily and is considered the most early branching of the three. It has a more complete chaetotaxy than the other subfamilies and is characterised by the fronto-orbital setae being lateroclinate over the margin of the eye, two postpronotal setae, 1 or 2 scapular setae, 1 supra-alar seta and 1 postsutural intra-alar seta (between supra-alar and dorsocentral line) and particularly by the male postabdomen, in which the sclerites anterior to the terminalia are asymmetrical. Siphonellopsinae is recognised as sister-group to the remainder of the Chloropidae combined. Siphonellopsinae are most diverse in the Southern Hemisphere (the Afrotropical, Australasian and Neotropical Regions). Generic limits within the subfamily remain unresolved. Andersson (1977) recognised five genera and Nartshuk (2012) four, but Sabrosky (1982) placed the Afrotropical species in the single genus *Apotropina*, which was followed by Wheeler (2010: 1149), for all Central American species. The question cannot be resolved without revision of the extralimital species and Sabrosky (1982) is followed here.

Tschirnhaus & Hoffeins (2009) listed two Chloropidae genera from Eocene Baltic amber: the extinct *Protoscinella* Hennig with several species and *Tricimba*. They included an identification key to species in amber and stated that wing crossvein *bm–m* was already lost in chloropids in Baltic amber. Evenhuis (2014) included seven fossil species in four genera from the Baltic Region, England, France and Germany.

Identification

The earliest comprehensive work on Afrotropical Chloropidae is the monograph by Becker (1910), which was excellent for the time, although the generic concepts are now out of date. The revision by Sabrosky (1951) in the Ruwenzori Expedition series covers far more than the material resulting from that Expedition alone and is still very useful, although its treatment of the smaller species of Oscinellinae is rather sparse. There has been no comprehensive account since that time, although many papers revise smaller groups or describe new species (Dawah *et al*. 2020; Deeming 1981*a*, 2003; Deeming & Al-Dhafer 2012; Kubík 2006; Kubík & Barták 2010, 2014; Mlynarek & Wheeler 2010; Nartshuk 2001, 2012, 2014; Riccardi & Tschirnhaus 2018; Tschirnhaus 2017; Wheeler & Solecki 2013).

Some diagnostic features important for the identification of Chloropidae and applied in the below identification key, but not present in all species, are as follows: (1) the ocellar tubercle (Figs 16, 19) – a raised area between and including the three ocelli; (2) the ocellar triangle (Fig. 13) – a triangular area on the frons, enclosing the ocelli and extending anteriorly, in some species to the anterior margin of the frons and laterally or in few genera covering the whole frons, but rarely difficult to distinguish on the frons; (3) the antennal foveae (Figs 14, 22) – rounded pits in which the antennae are set, often separated by a vertical facial carina; (4) the tibial organ (Fig. 159) – a discrete sensory area of minute microtrichia on the posterodorsal surface of the posterior tibia in some genera; and (5) the femoral organ (Fig. 160) – an area of short stubby setulae in males of some species or genera, situated on raised bases on the dorsal surface of the mid femur.

Head length is measured from the most posterior margin of the occiput to the most anterior margin of the head, *i*.e., either the frons or lunule or vibrissal angle. Depth is measured from the highest part of the frons (usually the ocellar tubercle), to the lower margin of the gena, excluding the proboscis.

Chloropidae may be collected using a variety of methods. Sweeping grasslands, wetlands and trees provide a variety of species. Flies are readily collected in Malaise and pan traps, or by insecticidal fogging of forest and savanna trees (see Chapter 2). They also occur at flowers, both at ground level and on shrubs and trees. Chloropidae are normally micro-pinned in the field for later staging and very small specimens can be point-mounted or reverse-pinned. Alternatively, specimens can be collected or preserved in 70 or 80% ethanol, for later drying and point-mounting, or preserved at higher ethanol concentrations and frozen for later DNA extraction (see Chapter 2). Specimens are best examined dry, as the patterns of pruinescence provide numerous diagnostic features. To date, few Chloropidae have been studied using combined molecular

and morphological methods, although a start has been made (Ismay & Ang 2019; Safonkin *et al*. 2017, 2018, 2020; Triseleva *et al*. 2014, 2020). Such combined studies may resolve issues of species complexes, particularly of pest species complexes, such as the genus *Hippelates* and the *Oscinella* (*O*.) *frit* complex.

Key to genera of Afrotropical Chloropidae

1. Wings and halteres absent or wings reduced to tiny stubs (e.g., Figs 27, 76) (OSCINELLINAE [in part]) . . . 2
– Wings and halteres present (e.g., Figs 26, 28–75, 77–126) 5
2. Scutum and scutellum clothed in long, erect spine-like setae, longer than head (Fig. 76); abdominal tergites 1 and 2 fused into one visible segment, convex and heavily sclerotised, all other tergites covered by segment (Fig. 76) (formerly *Myrmecosepsis*) . . . . . *Anatrichus* Loew [in part]
– Scutum and scutellum not clothed in long, erect spine-like setae; other characters not as above 3
3. Head with 2 fronto-orbital setae longer than remainder (Fig. 7); antennal arista thickened and pubescent (Fig. 7) . . . . . *Elachiptera* Macquart [in part]
– Head with fronto-orbital setae even in size, antennal arista slender, with long pubescence 4
4. First visible abdominal segment (tergite 1 + 2) elongated (Fig. 27), almost equal to combined length of following three visible segments, or head with ocellar triangle polished dark brown to black . . . . . *Alombus* Becker
– First visible abdominal segment not strongly elongated (Fig. 48), not longer than two following segments combined; head with ocellar triangle and thorax dull, densely grey pruinescent (*C. aptera* Sabrosky, 1951). . . . . *Conioscinella* Duda [in part]
5. Wing with costal vein (*C*) not extending to vein M_1, ending just beyond vein R_{4+5} or short of vein M_1 (e.g., Fig. 141) (in *Dicraeus* (Oscinellinae) at least non-Afrotropical species also have costal vein not reaching vein M_1 (e.g., Fig. 50)) 6
– Wing with costal vein (*C*) extending to vein M_1 (may be attenuated distally) (e.g., Fig. 148). 8
6. Wing with costal vein (*C*) extending almost to vein M_1, but with distinct gap distally (e.g., Fig. 141) (OSCINELLINAE [in part]). 7
– Wing with costal vein (*C*) extending to vein R_{4+5}, but may be extended ¼ distance to vein M_1 (e.g., Figs 150, 153) (CHLOROPINAE). 71
7. Thorax with anepisternum bare (Fig. 39); head with ocellar setae not proclinate and widely divergent; long axis of eye vertical (Fig. 39); wing with costal vein (*C*) extending halfway to vein M_1 (Fig. 39) (*C. abbreviata* Deeming, 2011) . . . . . *Calamoncosis* Enderlein [in part]
– Thorax with anepisternum setulose (as in Fig. 129); head with ocellar setae proclinate and widely divergent (as in Figs 16, 18); long axis of eye more or less diagonal (Fig. 95); wing with costal vein (*C*) extending more than quarter way to vein M_1 (Fig. 95) (*S. trapezoides*) . . . . . *Scoliophthalmus* Becker [in part]
8. Head with fronto-orbital setae usually long (Fig. 3), with upper one sometimes lateroclinate; ocellar setae proclinate and divergent; thorax with postpronotal lobe with 2 long, strong setae, inner one lateroclinate and outer one reclinate (Fig. 3); hind tibia with anteroventral comb; habitus as illustrated in Fig. 33 (SIPHONELLOPSINAE). . . . . *Apotropina* Hendel
– Thorax with postpronotal lobe usually with 1 seta, but if with more, then not arranged as above; other characters not as described above (OSCINELLINAE [in part]) 9
9. Abdomen reduced to 1 or 2 visible segments, convex and heavily sclerotised (e.g., Figs 29, 97) 10
– Abdomen not reduced, with 4 visible segments, not convex and heavily sclerotised (e.g., Figs 31, 32, 35, 38). 12
10. Prothorax not developed, without distinct dorsal transverse carina, with head and thorax closely applied (Fig. 29); scutum and scutellum clothed in long, erect setae, longer than head (Fig. 29) (*Anatrichus sensu stricto*) . . . . . *Anatrichus* Loew [in part]
– Prothorax expanded into neck-like structure between head and thorax, with distinct dorsal transverse carina; scutum and scutellum clothed in long, erect setae, longer than head or setae absent (e.g., Figs 76, 97). 11
11. Scutum and disk of scutellum clothed in long, erect setae, longer than head (Fig. 76) (formerly *Myrmecosepsis*) . . . . . *Anatrichus* Loew [in part]

– Scutum and disc of scutellum without long, erect setae (Fig. 97) . . . . . .*Sepsidoscinis* Hendel

12. Thorax with anepisternum setulose (e.g., Fig. 129) (very small in *Mimosepsis mallochi* Sabrosky, 1951); head with ocellar setae proclinate and divergent (as in Figs 16, 18); hind tibial organ absent 13

– Thorax with anepisternum not setulose, but with pruinescence or fine pile (without sockets at base) in some genera, or if with setulae (*Anomoeoceros*), then head with ocellar setae reclinate (e.g., Fig. 2), ocellar setae proclinate in some genera or otherwise directed; hind tibial organ present or absent 17

13. Habitus *Sepsis*-like (Fig. 75), with head 1.2 × as long as high, with axis almost horizontal; abdomen petiolate and abdominal segment 2 also strongly constricted basally (except in *M. scutellaris* Deeming, 1976); head with ocellar setae erect, subparallel or slightly converging. . . . . .*Mimosepsis* Sabrosky

– Habitus not *Sepsis*-like (e.g., Figs 78, 91, 95, 113, 120); head in almost all species higher than long; abdomen usually broad at base, abdominal segment 2 not constricted; ocellar setae long proclinate and widely divergent 14

14. Scutellum covering entire, or virtually entire abdomen, very large, rounded, broader at middle than at base, with numerous (> 6), pairs of setae inserted at regular intervals around scutellar margin (Figs 78, 120). . . . . *Nomba* Walker

– Scutellum conical or subconical, narrowing more or less regularly from base to apex, not expanded as above (shortly conical or rounded in a few species of *Rhodesiella*) (e.g., Figs 91, 95, 113); scutellar setae few in number, usually 1 pair of apical setae and 1–2 pairs of lateral setae (e.g., Figs 131, 132) 15

15. Antennal arista glabrous, without microtrichia or setulae; head with gena broad, highly polished, surface glabrous; eye with long axis more or less diagonal (Fig. 95) . . . . . *Scoliophthalmus* Becker [in part]

– Antennal arista distinctly pubescent (as in Fig. 24), although sometimes microscopically so; head with gena narrow, usually linear, if broader, then not smooth and glabrous; eye with long axis vertical . . . 16

16. Scutellum with 2–3 pairs of elongate, finger-like projections, each much longer than broad (from almost as long to longer than scutellum), bearing setae (Fig. 113) . . . . . *Dactylothyrea* de Meijere

– Scutellum without elongate, finger-like projections, in some species with distinct tubercles at bases of setae, projections distinctly shorter than remainder of scutellum (Figs 91, 131, 132) . . . . . .*Rhodesiella* Adams

17. Head with ocellar setae proclinate and divergent (e.g., Fig. 18) to parallel, not reduced in size. 18

– Head with ocellar setae erect to slightly reclinate (rarely proclinate, then reduced in size), usually convergent to cruciate (e.g., Figs 2, 8), rarely parallel 22

18. Head with postocellar setae parallel (Fig. 10); 2–3 fronto-orbital setae longer, equal to or longer than ocellar setae, remaining setae very small (Fig. 10); antennal postpedicel reniform (as in Fig. 12); wing with second costal sector (veins R_1 to R_{2+3}) *ca* 2 × as long as third sector (veins R_{2+3} to R_{4+5}); basal radial cell (*br*) not wider at separation of veins R_{2+3} and R_{4+5}; hind tibial organ present (as in Fig. 159) . . . . . .*Kwarea* Sabrosky

– Head with postocellar setae cruciate to inclinate (e.g., Figs 18, 24); fronto-orbital setae without 2–3 setae enlarged (e.g., Figs 18, 24), or if enlarged, then at most ¾ as long as ocellar setae, or if enlarged, then basal radial cell (*br*) wider at separation of veins R_{2+3} and R_{4+5} than at crossvein *r–m* (e.g., Figs 79, 90, 104, 108); hind tibial organ present or absent 19

19. Head with ocellar setae proclinate and slightly convergent (Fig. 24); most posterior fronto-orbital setae longer than several other enlarged upper fronto-orbital setae (Fig. 24); antennal postpedicel variable in form; wing cell *br* distinctly broadened at middle, where veins R_{2+3} and R_{4+5} separate (Fig. 108) . . . . . Undescribed genus A

– Without above combination of characters 20

20. Wing with second costal sector (veins R_1 to R_{2+3}) shorter or slightly longer than third sector (veins R_{2+3} to R_{4+5}) (Fig. 104). . . . . *Stenoscinis* Malloch [in part]

– Wing with second costal sector (veins R_1 to R_{2+3}) more than twice as long as third sector (veins R_{2+3} to R_{4+5}) (e.g., Fig. 90) 21

21. Wing vein M_1 with terminal section slightly curved, first towards vein R_{4+5} and then away from it; crossvein *r–m* in basal ¼ or ⅓ of cell *bm+dm*; cell *bm+dm* narrow and elongate (Fig. 79) . . . . . *Notaulacella* Enderlein

– Wing vein M_1 straight; crossvein *r–m* near middle of cell *bm+dm*; cell *bm+dm* broader (Figs 90, 151) . . . . . .*Psilacrum* Becker

22. Hind tibia with strong apical or anteroventral spur equal to, or longer than, diameter of tibia (e.g., Fig. 156) (doubtful cases key both ways). 23

– Hind tibia without apical or subapical spur, or if present, then this shorter than diameter of tibia . . . 26

23. Wing with apical section of vein M_1, curving first towards vein R_{4+5}, then away from it (Fig. 140); head with *ca* 6–7 reclinate, curved fronto-orbital setae developed (Fig. 35) . . . . *Arcuator* Sabrosky [in part]

– Wing with M_1 not as above (e.g., Figs 38, 61, 114); head with fronto-orbital setae differently arranged from above (e.g., Figs 7, 61) 24

24. Antennal arista thickened and blade-like (Fig. 7) (*E. acanthellata* Deeming & Al-Dhafer, 2012) . . . . . *Elachiptera* Macquart [in part]

– Antennal arista slender, setula-like (as in Fig. 17) (e.g., Fig. 38) 25

25. Scutellum as long as broad; antennal postpedicel reniform (Fig. 38); scutum shiny; head with ventral part of face without medial carina (as in Fig. 8); katepisternum with long dorsal seta (Fig. 130). . . . . *Cadrema* Walker

– Scutellum much broader than long; antennal postpedicel round (not reniform) (Fig. 61); scutum pruinescent (Fig. 61); head with blade-like facial carina well-developed (as in Fig. 12); katepisternum without dorsal seta. . . . . *Hippelates* Loew

26. Head with postocellar setae (= postvertical setae *sensu* Sabrosky 1951: 754), stout, straight, parallel (e.g., Fig. 9) (slightly convergent in *Anacamptoneurum*, Fig. 28), slightly reclinate; head with frons shiny, in some species dulled by micro-sculpture; ocellar triangle not sharply demarcated in some species; eye bare, long axis diagonal (e.g., Fig. 11); gena broad (except in *Heteroscinis* Lamb, as in Fig. 104), characteristically divided diagonally from vibrissal angle dorsally to occiput by slightly angled margin, in many species ventral part smooth and shiny (often with distinct setulae), dorsal part pruinescent (without setulae) (e.g., Fig. 11); wing crossvein *dm–m* at least slightly oblique (e.g., Figs 64, 138); in many species cell *br* strongly broadened (e.g., Fig. 138). 27

– Head with postocellar setae in most species erect and cruciate (e.g., Figs 8, 21), in some species only convergent, if parallel to subparallel, then eye densely pubescent (e.g., Fig. 2); eye pubescent in many species; other characters not as above 31

27. Antennal postpedicel acutely angulate at apex dorsally (Fig. 28); scutellum flat on disc, broadly rounded apically, semicircular in outline, with short (but longer than scutellum), approximated apical setae and *ca* 8 pairs of short lateral setae, barely longer than discal setulae (Fig. 133) . . . . . *Anacamptoneurum* Becker

– Antennal postpedicel rounded apically or weakly angulate (e.g., Figs 9, 11, 12); scutellum not as above, in most species more elongate and conical or subconical (e.g., Figs 54, 86); setae not as above 28

28. Scutum with fine punctures arranged in rows (in many species regular rows) (Fig. 60); head with face not carinate (as in Fig. 8); scutellum narrowly elongate conical, in most species raised above level of base, setae arising from lower margin (Fig. 60); thorax with notopleural setae 1 + 2 (as in Fig. 128) . . . . . *Heteroscinis* Lamb

– Scutum densely and strongly punctured (in many species not in regular rows) (e.g., Fig. 54); head with facial carina strong and distinct, although usually narrow (e.g., Fig. 12); scutellum broader, disc flattened or virtually so, setae not as above (e.g., Figs 54, 86); thorax with notopleural setae 1 + 1 or 1 + 3, or more, rarely 1 + 2 29

29. Thorax with notopleural setae 1 + 3 or more, rarely appearing as 1 + 2, with more posterior weaker and less distinct (as in Fig. 128); scutellum with lateral setae numerous (7–12 pairs), stout and all subequal in length (Fig. 86); legs slender (Fig. 86) . . . . . *Polyodaspis* Duda

– Thorax with notopleural setae 1 + 1; scutellum with lateral setae less numerous (usually 3–7 pairs); legs stout or slender (e.g., Figs 54, 64) 30

30. Legs stout (Fig. 54); fore femur enlarged, with posteroventral ridge with row of spines or denticles (Figs 54, 157) (very small in *E. nigrescens*; absent in *E. fascipennis*, an aberrant species distinguished by 3 black fasciae on wing); proboscis short, inconspicuous; head with frons smooth, without piliferous punctures or with a few minute ones, usually appearing glabrous. . . . . *Epimadiza* Becker

– Legs slender (Fig. 64); fore femur neither enlarged nor armed with spines or denticles; proboscis of various lengths, slender and elongate (Fig. 64); head with frons with evident piliferous punctures, often appearing as dark maculae in most species (Fig. 12) (formerly *Fiebrigella*) . . . . . *Lasiambia* Anonymous

31. Head with facial carina distinctly developed, usually separating bases of antennae, continued ventrally to lower facial margin (e.g., Figs 14, 22); antennal foveae concave (e.g., Figs 14, 22), sometimes deeply so; antennae small; postpedicel short and rounded (e.g., Figs 14, 22, 39, 81, 99, 109, 124). 32

– Head with facial carina absent in most species, if present, then low and incomplete, not reaching oral margin and face usually flat (*i.e.*, antennal foveae not concave) (as in Fig. 12); if carina developed, then

antennal postpedicel elongate, 2–4 × as long as broad (e.g., Fig. 116), or scutum with 3 deeply incised lines of punctures (e.g., Fig. 126), or head with ocellar triangle covered with deep pit-like punctures (e.g., Fig. 2) 38

32. Head and scutum with setae reduced in size, with setulae long, very numerous and dense, making distinguishing between these very difficult (Figs 14, 117); head with facial carina very strongly developed, broad and flat on anterior margin (Fig. 14) . . . . . *Lipara* Meigen

– Head and scutum with setae not reduced in size, easily distinguishable from setulae (e.g., Figs 39, 81, 99, 105, 109, 124); head with facial carina variously developed (e.g., Fig. 22) 33

33. Eye with long axis strongly diagonal; head elongate, distinctly longer than high (Fig. 105); thorax with notopleural setae 1 + 1; anepisternum and anepimeron with large shiny areas on ventral or posterior ½ (Fig. 105) (including *Aprometopis* Becker) . . . . . *Strobliola* Czerny

– Eye with long axis vertical or virtually so; head not elongate, higher than long (e.g., Figs 39, 81, 99, 109, 124); thorax with notopleural setae 1 + 1 or 1 + 2; anepisternum and anepimeron almost entirely shiny to almost entirely pruinescent (e.g., Figs 39, 99, 109) 34

34. Thorax with katepisternum, anepisternum and anepimeron almost entirely pruinescent, only minute shiny area on ventral margin (Fig. 109); notopleural setae 1 + 2 (as in Fig. 128); setae mostly thickened, white (Fig. 109) . . . . . Undescribed genus B

– Thoracic pleura more extensively shiny on katepisternum, anepisternum and anepimeron (e.g., Figs 39, 99); notopleural setae 1 + 1 or 1 + 2 35

35. Wing with vein R_{2+3} short; second costal sector (veins R_1 to R_{2+3}) much shorter than third sector (veins R_{2+3} to R_{4+5}) (Fig. 124), if second sector as long, or longer than third and vein R_{2+3} longer, then apical scutellar setae less than ½ length of scutellum; head setae minute, ocellar and postocellar setae erect and convergent; eye bare, or appearing so, at most with minute, sparse pubescence; proboscis short . . . . . *Siphunculina* Rondani

– Wing with vein R_{2+3} relatively long, second costal sector (veins R_1 to R_{2+3}), distinctly longer than third sector (veins R_{2+3} to R_{4+5}) (e.g., Figs 81, 99, 141); scutellum with apical scutellar setae at least as long as scutellum (as in Fig. 135); head setae longer, postocellar setae parallel to subparallel; eye densely long-pubescent to short setulose (can be sparse); proboscis usually slender, elongate and geniculate (e.g., Fig. 20, 37, 81, 99) (except in some *Calamoncosis*) 36

36. Head with ocellar triangle without setulae within lateral margins (as in Fig. 7). . . . . *Oscinimorpha* Lioy

– Head with ocellar triangle with setulae within lateral margins (as in Fig. 8) 37

37. Head with ocellar triangle with numerous strong pit-like punctures, about 3 rows inside lateral margin of triangle; eye with sparse microtrichia; thorax with notopleural setae 1 + 2 (as in Fig. 128). . . . . *Calamoncosis* Enderlein [in part]

– Head with ocellar triangle with single row of punctures within lateral margin (as in Fig. 2); eye with strong microtrichia (as in Fig. 2); thorax with notopleural setae 1 + 2 (as in Fig. 128) . . . . . *Siphonella* Macquart

38. Thoracic pleura entirely pruinescent on at least anepisternum, anepimeron and katepisternum (e.g., Figs 31, 32, 44, 68) 39

– Thoracic pleura more extensively shiny, at least anepisternum or anepimeron or katepisternum with extensive shiny area and anepimeron partly shiny or pleura more extensively shiny (e.g., Figs 58, 59, 88, 92). 41

39. Head with face deeply concave; upper part of facial carina triangular and overhanging face, carina only developed in dorsal part; head much deeper than long (Fig. 44); ocellar triangle indistinguishable; gena deep (Fig. 44); eye densely setulose; scutum with weakly developed median groove and weakly developed groove or dark band along dorsocentral line . . . . . *Caviceps* Malloch

– Without above combination of characters 40

40. Scutellum short and broad, posterior margin straight; apical scutellar setae not inserted on tubercles (Fig. 134); thorax with anterior and posterior notopleural setae equally well-developed; postpronotal seta shorter than notopleural setae (Figs 31, 32) . . . . . *Aphanotrigonum* Duda

– Scutellum trapezoidal; apical scutellar setae inserted on tubercles (posterior margin of scutellum appearing concave) (Fig. 136); thorax with notopleural setae 1 + 1; postpronotal and anterior notopleural setae very short (Fig. 68) . . . . . *Meijerella* Sabrosky

41. Scutum with median and dorsocentral lines with deeply incised rows of punctures (Fig. 126). . . . . .*Tricimba* Lioy

– Scutum without three lines of punctures or not so deeply incised, though present and more or less evident (especially in *Elachiptera*, Fig. 114, with broadened arista) 42

42. Head with ocellar triangle with numerous setulae in rows set in distinct pit-like punctures (Fig. 2); postocellar setae stout, straight, parallel, directed slightly posteriorly (Fig. 2) . . . . . *Anomoeoceros* Lamb [in part]

– Head with ocellar triangle smooth, or without rows of punctures set in pit-like punctures (e.g., Fig. 122); postocellar setae erect and convergent or cruciate, if parallel to subparallel, then setae slender and weak 43

43. Scutellum with apical setae inserted on finger-like projections or distinct tubercles (e.g., Figs 26, 114), or antennal arista flattened (e.g., Fig. 7) and/or blade-like, or both; thorax with notopleural setae usually, but not always 0 + 1 or 1 + 1 44

– Scutellum without either finger-like projections or distinct tubercles (e.g., Fig. 80); antennal arista not flattened or blade-like (e.g., Figs 6, 21); thorax with notopleural setae usually 1 + 2, rarely fewer. . . 50

44. Antennal arista flattened, sword-shaped, with long pubescence (e.g., Fig. 122); head with fronto-orbital setae even in size, none longer than remainder (e.g., Fig. 122) 45

– If arista flattened and sword-shaped, then 1–2 pairs of fronto-orbital setae enlarged, or scutellum longer than broad, with apical setae approximated (e.g., Figs 88, 123) 46

45. Scutellum much longer than broad, apical setae closely approximated, inserted on small tubercles, submarginal setae undeveloped (Fig. 122); wing without markings; male terminalia with epandrium not enlarged laterally into flanges . . . . . .*Pseudogampsocera* Sabrosky [in part]

– Scutellum rounded, not longer than broad, lateral scutellar setae developed; wing markings present in some males; male terminalia with epandrium enlarged laterally into flanges (Fig. 57) . . . . . *Gampsocera* Schiner

46. Scutellum with apical scutellar setae borne on 2 long processes, longer than, or subequal to, length of remainder of scutellum (Fig. 26); head with most posterior fronto-orbital setae slightly longer than remainder; antennal arista slender (basal ½ flattened and blade-like in one species), but with long pubescence (Fig. 26) . . . . . .*Allomedeia* Mlynarek & Wheeler

– Scutellum either with more than 1 pair of elongate processes or setae arising from margin of scutellum, either directly (e.g., Figs 48, 80, 100, 135, 137) or from tubercles (e.g., Fig. 114); other characters not as above 47

47. Scutellum elongate and conical, with closely approximated apical setae (Fig. 123), without distinct lateral setae; thorax with notopleural setae 1 + 2; head with outer vertical and postocellar setae subequal, much longer (1.5 ×) than remaining setae on posterior margin of head (Figs 88, 123) (atypical species with flattened arista) . . . . . *Pseudogaurax* Malloch [in part]

– Scutellum not as above, either trapezoidal or short and broadly rounded apically; apical scutellar setae not approximated, with 1–2 pairs of lateral scutellar setae (e.g., Figs 135, 137); head with setae not as above 48

48. Scutellum short and broadly rounded apically, disc convex, not flattened and trapezoidal with angled margin; setae slender, not arising from distinct tubercles; head with 2 pairs of enlarged fronto-orbital setae (Figs 65, 135) (formerly *Melanochaeta* Bezzi) . . . . . *Lasiochaeta* Corti [in part]

– Scutellum usually flattened and trapezoidal in outline, apically subtruncate; setae strong, arising from distinct tubercles or finger-like projections (Fig. 114); head with or without enlarged fronto-orbital setae . . . . . .*Elachiptera* Macquart [in part] 49

49. Head with all pairs of fronto-orbital setae fine and evenly sized, none much larger than remainder (formerly *Cyrtomomyia*) . . . . . *Elachiptera* Macquart [in part]

– Head with 1–2 pairs of fronto-orbital setae enlarged compared to remainder (Fig. 7); . . . . . *Elachiptera sensu stricto* [in part]

50. Head with 1–2 pairs of fronto-orbital setae enlarged compared to remainder; antennal arista slightly thickened 51

– Head with all pairs of fronto-orbital setae fine and evenly sized, none much larger than remainder (e.g., Fig. 6); antennal arista variable 52

51. Head with at least 2 pairs of fronto-orbital setae enlarged, posterior seta longer than anterior; scutum flattened on disc (Fig. 55); scutellum with apical setae dorsally directed; head with postocellar setae slightly divergent; antennal postpedicel pointed apically (Fig. 55); habitus illustrated in Fig. 55. . . . . *Eribolus* Becker

– Head with 2 pairs of equal fronto-orbital setae enlarged, compared to remainder; scutum convex on disc; scutellum with apical setae posteriorly directed; head with postocellar setae convergent; antennal postpedicel not pointed apically; habitus as in Fig. 65, except arista not blade-like (species without strongly thickened arista) (formerly *Melanochaeta* Corti) . . . . . *Lasiochaeta* Corti [in part]

52. Scutellum with apical setae closely approximated, without lateral marginal setae (in most species), or these not distinct from setulae; scutellum clearly elongate (much longer than wide), conical, tapering to narrow apex (e.g., Fig. 123), if scutellum rarely short and broadly rounded (as in *Pseudogaurax dissimilipes* (Malloch, 1931)), then disc strongly flattened; eye and antennal arista with dense, long pubescence to short setulae 53

– Scutellum with apical setae usually widely separated basally, with 1–2 pairs of lateral setae; scutellum shorter than wide and usually broadly rounded in outline (e.g., Figs 80, 137); eye and antennal arista short-pubescent to bare 55

53. Antennal postpedicel not reniform, 1.1–1.6 × as long as deep; arista inserted near base of postpedicel (Fig. 2); head with postocellar setae parallel (Fig. 2), slightly reclinate; scutellum elongate and conical, *ca* 0.6 × as long as scutum (*A. flavipalpis* Sabrosky, 1951) . . . . . *Anomoeoceros* Lamb [in part]

– Antennal postpedicel reniform, deeper than long; arista inserted far from base of postpedicel (e.g., Fig. 122), or if postpedicel unusually long (as in *Pseudogaurax longicornis* Sabrosky, 1946), then prolonged dorsally and arista inserted at apex (e.g., Fig. 88); head with postocellar setae cruciate (e.g., Fig. 123) (except in *Pseudogaurax aberrans* Sabrosky, 1951); scutellum variable 54

54. Antennal arista strongly flattened laterally, long-pubescent dorsally and ventrally (Fig. 122); scutellum much longer than wide, disc convex, only 1 pair of approximated, apical setae (Fig. 122); head with inner vertical seta about equal in length to postocellar seta; outer vertical seta *ca* 1.5 × length of either . . . . . .*Pseudogampsocera* Sabrosky [in part]

– Antennal arista and scutellum variable; head with outer vertical and postocellar setae enlarged and subequal; inner vertical setae smaller than either, remaining setae along posterior margin of head much smaller than outer vertical and postocellar setae (Fig. 123) . . . . . *Pseudogaurax* Malloch [in part]

55. Antenna elongate; postpedicel longer than deep at middle (e.g., Fig. 116) 56

– Antenna not elongate; postpedicel not longer than deep at middle (e.g., Figs 6, 8) 57

56. Antennal postpedicel *ca* 4 × as long as deep, dorsal margin slightly concave (in lateral view) (Figs 67, 116); head with ocellar triangle shiny, extending broadly to anterior margin of frons (Fig. 67); face without carina; scutellum shorter than broad and trapezoidal (Fig. 116); eye bare . . . .*Leucochaeta* Becker

– Antennal postpedicel from as long as deep to several × longer than deep, exceeding height of face (Figs 17, 87); head with ocellar triangle heavily pruinescent to shiny, not extending to anterior margin of frons; face with carina barely discernible and without antennal foveae (Fig. 17); scutellum rounded; eye pubescent (Fig. 17) . . . . . .*Pselaphia* Becker

57. Wing with second costal sector (veins R_1 to R_{2+3}) 2.5 × as long as third sector (veins R_{2+3} to R_{4+5}) (Fig. 50); vein R_{2+3} parallel to vein R_{4+5} for most of length (Fig. 50). . . . . *Dicraeus* Loew

– Wing with second costal sector (veins R_1 to R_{2+3}) < 2.5 × as long as third sector (veins R_{2+3} to R_{4+5}) (e.g., Figs 145, 147, 148); vein R_{2+3} not parallel to vein R_{4+5} for most of length (e.g., Figs 145, 147, 148) . . . 58

58. Wing with first costal sector (*bcost* to vein R_1), longer than second sector (veins R_1 to R_{2+3}); crossvein *r–m* at close to ½ length of wing; crossvein *dm–m* strongly oblique (Figs 43, 142) . . . . . *Camptoscinella* Sabrosky

– Wing with first costal sector (*bcost* to vein R_1), shorter than second sector (veins R_1 to R_{2+3}); crossvein *r–m* in basal ½ of wing; crossvein *dm–m* only slightly oblique or upright (e.g., Figs 147, 148) 59

59. Body, wing and legs long, narrowed (Figs 103, 104); wing with anal lobe greatly reduced, appearing petiolate (Figs 103, 104); eye large and gena linear (Figs 103, 104); head with ocellar setae small and proclinate in some species . . . . . *Stenoscinis* Malloch [in part]

– Body, wing and legs shorter and stouter, not narrowed (e.g., Figs 35, 94); wing with anal lobe developed (e.g., Figs 140, 148); eye smaller and gena broader in most species (e.g., Fig. 74); head with ocellar setae erect and cruciate (e.g., Fig. 8) 60

60. Antennal postpedicel reniform, deeper than long (Fig. 58); wing cell r_1 short and broad, opposite end of vein R_1 much broader than cell r_{2+3} (Fig. 145); vein R_{2+3} distinctly concave anteriorly (Fig. 145); costal cell (*c*) unusually broad, *ca* 2 × as wide as distal portion of cell *br* (Fig. 145) . . . . . .*Gaurax* Loew

– Antennal postpedicel not reniform, *ca* as long as deep (e.g., Fig. 8); wing cell r_1 not broader opposite end of vein R_1 than cell r_{2+3} (e.g., Fig. 148); costal cell (*c*) only slightly broader than distal portion of cell *br* (e.g., Fig. 147) 61

61. Antennal arista blade-like and thickened, with dense microtrichia (Figs 25, 110); head with ocellar setae inserted outside ocellar tubercle, erect and long, at least as long as outer vertical setae . . . . . Undescribed genus C

– Antennal arista slender, not blade-like and thickened, with short microtrichia or bare (e.g., Figs 6, 21); head with ocellar setae inserted within ocellar tubercle, not erect, shorter than vertical setae (e.g., Figs 6, 21). 62

62. Wing with apical section of vein M_1 curving first towards vein R_{4+5} and then away from it (e.g., Fig. 140). 63

– Wing with vein M_1 not as described above (e.g., Fig. 148) 64

63. Thoracic pleura yellow, with black macula on ventral anepisternum; head with 4–7 strong reclinate curved fronto-orbital setae (Fig. 35) (species with or without short/fine apical, ventral tibial spur) . . . . . *Arcuator* Sabrosky [in part]

– Thoracic pleura black, without black macula on ventral anepisternum (Fig. 94); head with 4 weak fronto-orbital setae; hind tibia without spur (*S. sinuata* Deeming & Al-Dhafer, 2012) . . . . . *Sabroskyina* Beschovski [in part]

64. Head with ocellar triangle shiny, with one or more rows of small setulae within lateral margin (Fig. 8) . . . . . .*Hapleginella* Duda

– Head with ocellar triangle shiny or pruinescent, without row of small setulae within lateral margin (e.g., Figs 6, 21) 65

65. Head with ocellar triangle pruinescent (e.g., Figs 6, 21) 66

– Head with ocellar triangle shiny (as in Fig. 8) 69

66. Proboscis elongate, longer than head depth; head with gena with acute anterior angle, extended anteriorly to anterior margin of eye (Fig. 106) . . . . . *Trachysiphonella* Enderlein

– Without above combination of characters 67

67. Thorax either with notopleural setae 1 + 1 (then scutal setulae arranged in longitudinal rows), or notopleural setae 1 + 2 (with frons greatly inflated above dorsal margin of male eye; *M. dimorphica* Deeming & Al-Dhafer, 2012, Fig. 74) (including *Incertella*). . . . . *Microcercis* Beschovski

– Thorax with notopleural setae 1 + 2; scutal setulae not arranged in longitudinal rows in most species and head with frons not inflated above dorsal margin of male eye (e.g., Fig. 6). 68

68. Head with frons variable, from black to yellow; ocellar triangle usually pruinescent (may be shiny in some species) (Fig. 6); scutellum with setulae not extending over lateral margin (Fig. 48); male terminalia not as below . . . . . *Conioscinella* Duda [in part]

– Head with frons grey, with setulae set in darker maculae; ocellar triangle pruinescent (Fig. 21); scutellum with setulae extending over lateral margin (Figs 100, 137); male terminalia with black, shiny, globular surstylus . . . . . *Speccafrons* Sabrosky

69. Wing cell *br* greatly broadened at mid length (Fig. 94) (*S. aharonii*). . . *Sabroskyina* Beschovski [in part]

– Wing cell *br* not greatly broadened at mid length (e.g., Fig. 147) 70

70. Scutum with setulae arranged in regular longitudinal lines, separated by greater distance than length of setulae; habitus as illustrated in Fig. 80 . . . . . .*Oscinella* Becker

– Scutum with setulae irregularly arranged, not appearance of longitudinal rows of setulae, separated by less distance than length of setulae; habitus as illustrated in Fig. 92 . . . . . *Rhopalopterum* Duda

71. Hind femur thickened, > 2 × as broad as tibia, thicker than at least one other femur; hind tibia correspondingly curved (e.g., Figs 82, 158) 72

– Hind femur < 2 × as broad as tibia; if thickened, then all femora subequal in thickness; hind tibia not curved (e.g., Fig. 93) 76

72. Antennal arista broadened, or at least, with long dense microtrichia, appearing broad (Fig. 82) . . . . . .*Pachylophus* Loew

– Antennal arista slender, with short or minute pubescence (as in Fig. 15) 73

73. Head with anterior margin of frons extended anteriorly to anterior margin of eye; ocellar triangle occupying almost entire frons, with numerous setulae placed in small pit-like punctures; antennal arista white (Fig. 85) . . . . . .*Platycephala* Fallén [in part]

– Head with anterior margin of frons extended < 0.5 × length of eye; ocellar triangle triangular not occupying most of frons; antennal arista dark (e.g., Fig. 119) 74

74. Head with ocellar triangle without setulae within lateral margin; parafacial broader, visible in lateral view (Fig. 72); male terminalia with postgonites projecting. . . . . .*Meromyza* Meigen

– Head with ocellar triangle with setulae within lateral margin (as in Fig. 8); parafacial narrower, not visible in lateral view; male terminalia with postgonites not projecting 75

75. Hind femur with anteroventral row of strong, thorn-like spines (Figs 154, 155). . . . . *Archimeromyza* Deeming

– Hind femur without strong anteroventral row of thorn-like spines, with double row of minute, blunt, black ventral spines (Fig. 158) . . . . . .*Meromyzella* Andersson

76. Antennal arista thickened, usually flattened and blade-like (e.g., Fig. 84), or appearing thickened due to dense microtrichia, invariably entirely black. 77

– Antennal arista not thickened and flattened, although usually more or less pubescent (e.g., Figs 5, 13, 15, 30), some species with white, densely pubescent arista (appearing thickened) 83

77. Thorax with anepisternum with numerous setulae (e.g., Fig. 41); head depressed, much longer than high; frons with anterior margin projecting; eye with long axis virtually horizontal (e.g., Fig. 41) 78

– Thorax with anepisternum bare; head not depressed (except in *Mepachymerus* Speiser *sensu lato*); frons slightly projecting (e.g., Figs 52, 84); eye with long axis not horizontal (e.g., Fig. 84). 79

78. Wing surface convex; vein R_{2+3} fused with, or in contact with, vein R_1 and costal vein (*C*) throughout length; vein R_{4+5} strongly bowed anteriorly to vein R_{2+3}; vein M_1 ending at wing tip; scutellum with apical setae displaced to dorsal surface (Figs 40, 41). . . . . *Camarota* Meigen [in part, most]

– Wing surface flat; vein R_{2+3} narrowly separated from vein R_1 and later costal vein (*C*); vein R_{4+5} closer to wing tip than vein M_1; scutellum with apical scutellar setae positioned at margin (Fig. 42) (*C. cylindrica* Deeming, 1981) . . . . . .*Camarota* Meigen [in part]

79. Wing crossveins *dm–m* and *r–m* closely approximated (e.g., Fig. 96), separated by distance less than length of *dm–m* 80

– Wing crossveins *dm–m* and *r–m* not approximated (e.g., Fig. 70), separated by distance much greater than length of *dm–m* 81

80. Scutum with 1 pair of strong, black prescutellar dorsocentral setae (Fig. 52) . . . .*Elachiptereicus* Becker

– Scutum with 3 pairs of strong, black dorsocentral setae (Fig. 96) . . . . . .*Semaranga* Becker

81. Head with ocellar triangle with main part triangular, extending ½ to ⅔ length to anterior margin, with sinuate lateral margins and linear extension to anterior margin of frons; head slightly higher than long (Fig. 84); body, legs and wing not elongate; thorax almost as deep as long (Fig. 84); 2 or more fronto-orbital setae present on posterior part of frons . . . . . .*Phyladelphus* Becker

– Head with ocellar triangle usually with broad anterior margin, without linear anterior extension and without strongly sinuate lateral margins; head slightly longer than deep (Fig. 70); body, legs and wing more or less narrowly elongate (Fig. 70); only 2 fronto-orbital setae present. 82

82. Head with ocellar triangle reaching anterior margin of frons, either broadly, or terminating in point, always without linear extension and lateral margins invariably straight, main part pruinescent, with strong, shiny ridge along each lateral margin; thorax almost entirely pruinescent, pleura mostly pruinescent (Fig. 70); thoracic setae strongly reduced; most species with only 1 (posterior) notopleural seta (Fig. 70); thorax distinctly longer than deep (Fig. 70); legs very long, slender with laterally compressed anterior tarsi (Fig. 70); tibial organ absent; male terminalia with pregonite and postgonite discrete . . . . . *Mepachymerus* Speiser

– Head with ocellar triangle broadly reaching anterior margin, posterior margin almost as wide as frons, entirely shiny, without ridge along almost straight lateral margin (Fig. 101); thorax shiny at least on pleura; thoracic setae well-developed, usually with at least notopleural setae 1 + 2 (Fig. 101); legs not so elongate and anterior tarsi not laterally compressed (Fig. 101); tibial organ present; male terminalia with pregonite and postgonite fused . . . . . .*Steleocerellus* Frey

83. Head and thorax clothed in dense long setulae, much longer than length of postpedicel; anterior margin of frons considerably produced anterior to eye (Figs 23, 107). . . . . *Trichieurina* Duda

– Head and thorax without dense long setulae longer than length of postpedicel (e.g., Figs 13, 15, 19); anterior margin of frons produced anteriorly (in some genera) (e.g., Figs 19, 93). 84

84. Wing membrane either distinctly darkened, or with wide dark fascia along anterior margin to tip (e.g., Fig. 47) or abdomen ant-like and antenna short (not elongate). 85

– Wing membrane hyaline or very slightly darkened (e.g., Fig. 46); if abdomen ant-like, then antenna elongate. 86

85. Head and scutum black or dark brown, at most with thin pale fasciae (Fig. 47); male tergite 5 absent, or represented by pair of small crescent-shaped sclerites (Fig. 47) . . . . . *Chromatopterum* Becker

– Head and scutum yellow; scutum with black presutural macula on either side (Fig. 121); male tergite 5 as strongly developed as tergite 4 . . . . . *Pseudochromatopterum* Deeming

86. Head with frons greatly produced anteriorly (Figs 19, 93); ocellar triangle bare (Fig. 19); large species (body length: *ca* 4 mm) (Fig. 93) . . . . . *Sabeurina* Deeming

– Without above combination of characters 87

87. Wing without crossvein *dm–m* (Fig. 53) . . . . . *Diplotoxa* (*Elliponeura* Loew)

– Wing with crossvein *dm–m* (e.g., Figs 51, 89) 88

88. Wing with crossveins *r–m* and *dm–m* closely approximated, separated by distance less than length of *dm–m* (e.g., Fig. 51) 89

– Wing with crossveins *r–m* and *dm–m* not closely approximated, separated by distance much greater than length of *dm–m* (e.g., Figs 77, 83) 90

89. Head with ocellar triangle shiny (Fig. 51) . . . . . *Diplotoxa sensu stricto*

– Head with ocellar triangle pruinescent (as in Fig. 6) . . . . . *Diplotoxa* (*Pseudopachychaeta* Strobl)

90. Pale, heavily pruinescent, yellow species, with 3 broad, dull, reddish grey to black fasciae on scutum and 2 broad fasciae on abdomen (may appear darkened) (Fig. 73); head with ocellar triangle yellow, with large, round black macula anterior to ocelli; antenna 1.3–1.5 × as long as deep; arista white; head with gena broad, broader than depth of postpedicel (Fig. 73); body with white setae and setulae; scutellum flat dorsally. . . . . *Metopostigma* Becker

– Without above combination of characters 91

91. Antennal postpedicel distinctly lengthened, at least 1.5 × as long as deep (e.g., Fig. 85). 92

– Antennal postpedicel not distinctly lengthened, at most 1.25 × as long as deep (as in Fig. 24) 99

92. Head with frons extended anteriorly by ½ length of eye (measured from anterior margin of eye) (Fig. 85); ocellar triangle occupying almost entire frons, except narrow lateral fascia bearing fronto-orbital setae (Fig. 85); ocellar triangle clothed in small setulae set in small pit-like punctures; yellow species with dark marks on postpronotal lobe and ocellar tubercle (Fig. 85) (*P. scapularum* (Becker, 1907)) . . . . . *Platycephala* Fallén [in part]

– Without above combination of characters 93

93. Thoracic pleura with silver diagonal fascia (Fig. 77); antennal segments greatly lengthened (longer than eye) (Fig. 77) . . . . . *Neoloxotaenia* Sabrosky

– Thoracic pleura without diagonal silver fascia; antennal segments elongate (from not longer than eye to longer than eye) (e.g., Figs 1, 83) 94

94. Hind tibia with distinct tibial organ, comprising discrete sensory area of minute microtrichia on postero-dorsal surface (as in Fig. 159) 95

– Hind tibia uniformly setulose, without distinct tibial organ (some species with dark macula in organ position) 97

95. Wing cell *bm+dm* much narrower than cell *br* (Fig. 46); head with gena < 0.5 depth of eye (Fig. 46); thorax with anepisternum bare, or with at most, some black setulae; scutellum without approximated apical setae; male terminalia with band-shaped sclerites lateral to anus. . . . *Chloropsina* Becker [in part]

– Wing cell *bm + dm* not narrower than cell *br* (e.g., Fig. 37); head with gena > 0.5 depth of eye (e.g., Fig. 37); thorax with anepisternum bare or setulose; scutellum without approximated apical setae; male terminalia without band-shaped sclerites lateral to anus 96

96. Thorax with anepisternum with long, silvery white, thickened, reflective setulae over entire surface (Fig. 37); head, thorax and abdomen almost entirely clothed in thickened brilliant silvery white setulae, without black setulae (Fig. 37) . . . . . *Bathyparia* Lamb

– Thorax with anepisternum bare (Fig. 56); head, thorax and abdomen with pale to dark setae, never brilliantly reflective white (habitus as in Fig. 56, but yellow) (*E. longicornis* Deeming & Al-Dhafer, 2012) . . . . . *Eutropha* Loew [in part]

97. Antennal arista black, slender, any pubescence short and sparse (Fig. 111); scutum more or less shiny black (Figs 36, 111); apical scutellar setae not approximated (Fig. 111) . . . . . *Assuania* Becker

– Antennal arista white, densely pubescent, appearing slightly thickened; basal antennal segments yellow in many species (e.g., Fig. 83); scutum either dull black or with dull black fasciae (e.g., 63, 83); apical scutellar setae not approximated 98

98. Scutum in most species (except *L. opaculum* Becker, 1910), entirely black, not fasciate (Fig. 63); antennal pedicel elongate; postpedicel usually long and narrow (Fig. 63); male terminalia with postgonites short; pregonite and postgonites in alignment . . . . . *Lagaroceras* Becker

– Scutum yellow with black fasciae (Fig. 83); antennal pedicel not elongate; postpedicel slightly longer than deep (Fig. 83); male terminalia with pregonite and postgonites parallel; postgonite long. . . . . .*Parectecephala* Becker

99. Hind tibia with distinct tibial organ (as in Fig. 159), comprising discrete sensory area of minute microtrichia on posterodorsal surface 100

– Hind tibia without distinct tibial organ, uniformly setulose 104

100. Head unusually large, broader than thorax (e.g., Figs 62, 71, 118); eye large, occupying almost entire head in profile; gena linear (e.g., Figs 62, 71, 118); scutum smooth and shiny, strongly convex (in lateral view), extending as far above ventral margin of notopleuron as ventral margin of katepisternum below, setulae greatly reduced or absent, including on scutum and scutellum (e.g., Figs 62, 71, 118) 101

– Head not disproportionately large and broader than thorax (e.g., Figs 45, 69); eye not occupying entire head; gena not linear (e.g., Figs 45, 69); scutum (in lateral view) not strongly convex, with distinct setulae on scutum and scutellum (in most species) (e.g., Figs 45, 69) 102

101. Scutum very strongly arched, appearing hemispherical, appearing entirely bare of setulae (Fig. 62); dorsocentral setae absent; head without setae on frons, vertex and occiput, except minute fronto-orbital setae (Fig. 62) . . . . . *Homops* Speiser

– Scutum rounded, not hemispherical (Fig. 71); dorsocentral setae minute, with reduced setulae along dorsocentral lines and area broadening out posteriorly, bare centrally and lateral to dorsocentral lines (Fig. 118); head with minute setae on frons and vertex (Figs 16, 71, 118). . . . .*Merochlorops* Howlett

102. Scutellum slightly convex on disc, with lateral margin smoothly curved (Fig. 49); apical scutellar setae not strongly approximated; antennal postpedicel about as long as deep, slightly pointed dorsoapically (Fig. 49); mostly black species; tarsi yellow; head with ocellar triangle large, dulled by micro-sculpture (Fig. 49) . . . . . .[*Cryptonevra* Lioy]

– Scutellum flattened on disc with lateral margin angled (e.g., Fig. 125); apical scutellar setae closely approximated (e.g., Fig. 125); antennal postpedicel rounded; mostly yellow or partly black species; remaining characters not as above (e.g., Fig. 125). 103

103. Small, partly black species (body length: < 3 mm) (Fig. 125); antennal postpedicel with apex variable in colour; head with gena < 0.5 depth of eye . . . . . .*Thaumatomyia* Zenker

– Large, yellow species (body length: > 4 mm), only black on maculae lateral to ocelli and at tip of ocellar triangle; antennal postpedicel with apex darkened; head with gena > 0.5 depth of eye. . . . . Undescribed genus D

104. Head with fronto-orbital setae reduced to 3–4 slightly enlarged pairs (e.g., Fig. 13); male terminalia with surstylus at least partially fused to epandrium. 105

– Head with more than 3–4 pairs of fronto-orbital setae, graduated in size (e.g., Fig. 45); male terminalia with surstylus free from epandrium 106

105. Antennal arista black (Figs 13, 66) . . . . . *Lasiosina* Becker

– Antennal arista white (Fig. 102) . . . . . .*Stenophthalmus* Becker

106. Large, robust species (body length: 4.0–5.5 mm and up to 2 mm broad) (Fig. 98); scutum and scutellum with small seed-like swellings at base of setulae (Fig. 98) . . . . . .*Siphlus* Loew

– Without above combination of characters 107

107. Head with vibrissal angle extended anteriorly, strongly acute to right-angled (Figs 15, 69). . . . . .*Melanum* Becker

– Head with vibrissal angle not extended, not strongly acute to right-angled (e.g., Fig. 46). 108

108. Wing cell r_{2+3}, at level of crossvein *dm–m*, much narrower than cell r_{4+5} (Fig. 46); head with gena < 0.5 depth of eye (Fig. 46); cell *bm+dm* narrow (Fig. 46); male terminalia with band-shaped sclerites lateral to anus . . . . . *Chloropsina* Becker [in part]

– Without above combination of characters 109

109. Wing cell r_{2+3} at apex of vein R_1, subequal to cell r_{4+5} (Fig. 56); head with gena equal to 0.5 or more of eye depth (Fig. 56); male terminalia without band-shaped sclerites lateral to anus . . . . . *Eutropha* Loew [in part]

– Without above combination of characters 110

110. Head with ocellar triangle pruinescent, with 3–4 distinct lateral grooves within lateral margin (Fig. 30); ocellar tubercle pruinescent; antennal postpedicel slightly longer than deep, arista white (Fig. 30); male terminalia with posterior corner of epandrium projecting and granulate . . . *Anthracophagella* Andersson

– Head with ocellar triangle shiny to pruinescent, lateral margins either smooth or with indistinct lateral grooves (Figs 5, 112); ocellar tubercle pruinescent in some species; antennal postpedicel slightly longer than deep to as long as deep; arista black in most Afrotropical species (Figs 45, 112); male terminalia with posterior lateral corner of epandrium neither projecting nor granulate . . . . . *Chlorops* Meigen

Synopsis of the fauna

The family Chloropidae includes 3,056 valid species worldwide (M. von Tschirnhaus, pers. comm. 2021), but the true figure is much higher, perhaps 7,000 species. Exactly 200 genera are recognised globally and it is regarded as an "open-ended taxon". In the Afrotropical Region, there are 454 described species in 88 genera, four undescribed genera and at least 160 undescribed species are known. This figure is, however, an underestimate of the true species richness of the family in the Afrotropics, as every new study reveals numerous new species.

***Allomedeia* Mlynarek & Wheeler** (Oscinellinae)**.** An endemic genus of five described species (Fig. 26), distributed in Kenya, Nigeria, South Africa and Uganda (Mlynarek & Wheeler 2010). Three additional undescribed species are known from Nigeria and South Africa. Confirmatory characters include: arista with long microtrichia, simple, not thickened, but blade-like in basal half (in one species) (Fig. 26); facial carina undeveloped; ocellar triangle without setulae or punctures; ocellar setae erect and cruciate; postocellar setae cruciate; thoracic pleura extensively shiny (Fig. 26); anepisternum bare; apical scutellar setae borne on tubercles that differ from barely discernible to *ca* as long as scutellum (Fig. 26); and hind tibial spur absent, tibial organ present on hind tibia, femoral organ on mid femur absent. The biology of the genus and immature stages remain unknown. The genus can be distinguished from *Disciphus* Becker (a widespread genus in the Oriental Region), by the lack of a femoral organ and the lack of an enlarged posterior fronto-orbital seta and in having the cerci in the male medially fused into a single mesolobus. Mlynarek & Wheeler (2010) provided an identification key.

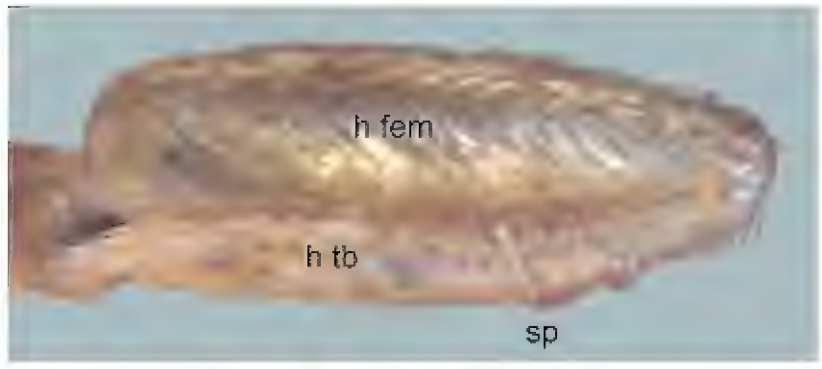
***Alombus* Becker** (Oscinellinae)**.** An endemic genus of 11 valid species (Fig. 27), confined to the continental Afrotropics (Evenhuis & Pape 2020), distributed in Central and East Africa, with most records from higher elevations. Confirmatory characters include: loss of wings and halteres (Fig. 27); the simple, not thickened arista; reduced head and thoracic setation (partly due to loss of wings); and the fused first and second abdominal segments (Fig. 27) longer than remainder of abdomen, but remaining segments visible (if fused segments not longer than remainder of abdomen, then ocellar triangle shiny dark brown to black). Biology and immature stages remain unknown. Richards (1955, 1962, 1965) provided identification keys to the known species.

***Anacamptoneurum* Becker** (Oscinellinae)**.** Four valid species were known from the Afrotropical and Oriental Regions, before Cherian (2012) described several more from India (Evenhuis & Pape 2020). One species, *A. obliquum* (Fig. 28), is known from the Afrotropical Region, recorded from Botswana, Nigeria, Sudan and Tanzania (Evenhuis & Pape 2020). Cherian (2012) sank *Fiebrigella* (now *Lasiambia* in the Afrotropical and Palaearctic Regions) and *Polyodaspis* as junior synonyms of *Anacamptoneurum*, but Bazyar *et al*. (2015), Ebejer & Andrade (2015), Nartshuk (2016) and Nartshuk *et al*. (2020) treated these as separate genera. In concurrence with those authors, these are here retained as separate genera. Confirmatory characters include: postpedicel acutely angulate at apex dorsally (Fig. 28); eye bare, with long axis diagonal; gena broad, divided diagonally from vibrissal angle dorsally to occiput; ocellar setae reclinate and convergent; postocellar setae stout, straight, slightly convergent, slightly reclinate; anepisternum bare; scutellum flat on disc, broadly rounded apically (semicircular in outline), with closely approximated apical setae short (but longer than scutellum) and *ca* eight pairs of short lateral setae, barely longer than discal setulae (Fig. 133); wing crossvein *dm–m* at least slightly oblique (Fig. 138); and posterior tibia without a spur. This small, shiny black species has been reared from a variety of cultivated cereal crops and grasses (Deeming 1972: 21), but the immature stages remain unknown. An identification key, including characters for *A. obliquum*, was provided by Cherian (2012).

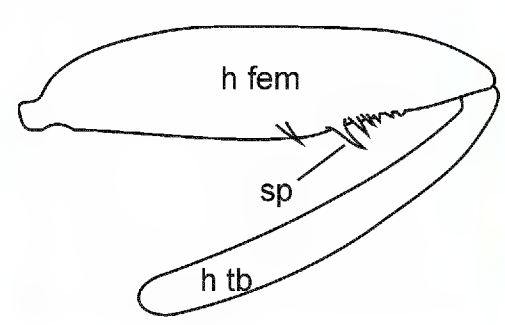
***Anatrichus* Loew** (Oscinellinae)**.** A genus of five, predominantly black valid species (Figs 29, 76), occurring in the Afrotropical, Australasian, Oriental and Palaearctic Regions (Evenhuis & Pape 2020; M. von Tschirnhaus, pers. comm. 2021). The genus also includes three Oriental species (Cherian 2012), formerly placed in *Myrmecosepsis*, which was recently synonymised with *Anatrichus* by Mlynarek & Wheeler (2018) and following publication of the identification key to brachypterous flies by Marshall *et al*. (2017: 353). Three described species are known from the Afrotropical Region: *A. bimaculatus* Kubík & Barták, 2010, described from Zambia; the widely distributed species, *A. erinaceus* and *A. pygmaeus* recorded from Ethiopia, Gambia, Liberia and Nigeria (Deeming & Al-Dhafer 2012) and at least one undescribed apterous species is known from Nigeria (J.C. Deeming, unpubl.). The species formerly placed in *Myrmecosepsis* differ from the winged Afrotropical *Anatrichus* in having one very long and strong vertical seta developed. The prothorax is developed into a neck-like structure between the head and thorax with a distinct transverse carina. The wing and halter are lacking. These species are keyed out separately in the above identification key. Confirmatory characters for the remaining *Anatrichus* species include: the head and thorax closely approximated (Figs 29, 76); scutum and scutellum with dense, long, erect setae (longer than head), but absent on

abdomen (Figs 29, 76); prothorax undeveloped; and abdominal segments 1 + 2 fused, heavily sclerotised, convex dorsally, covering remaining smaller segments (Figs 29, 76). There are apterous, brachypterous and winged species. The larva has been found to occur in the stems of Poaceae, including rice, Sorghum and Wheat (Deeming & Al-Dhafer 2012; Ferrar 1987: 107), but it is unclear whether it is a primary invader or occurs secondarily in damaged plant tissue. It has been reared from the malvaceous fibre crop Kenaf, *Hibiscus cannabinus* L. (Malvaceae), in Nigeria when damaged by *Alcidodes* Marshall (Coleoptera: Curculionidae) (J.C. Deeming, unpubl.). Nartshuk (2010*b*) described and figured the puparium, cephaloskeleton and prothoracic spiracles of *A. pygmaeus*. Kubík & Barták (2010) distinguished *A. bimaculatus* and *A. erinaceus* and Deeming & Al-Dhafer (2012) provided an identification key to distinguish *A. erinaceus* and *A. pygmaeus*.

Anomoeoceros **Lamb** (Oscinellinae)**.** An endemic genus of four dark-bodied valid species, distributed in Central, East, Southern and West Africa (Evenhuis & Pape 2020). Two species are distinctive, with the ocellar triangle bearing strongly developed setulae set in distinct pit-like punctures (Fig. 2), whereas in the other two species these are restricted to two rows along the margins of the triangle. Confirmatory characters include:



154 *Archimeromyza*

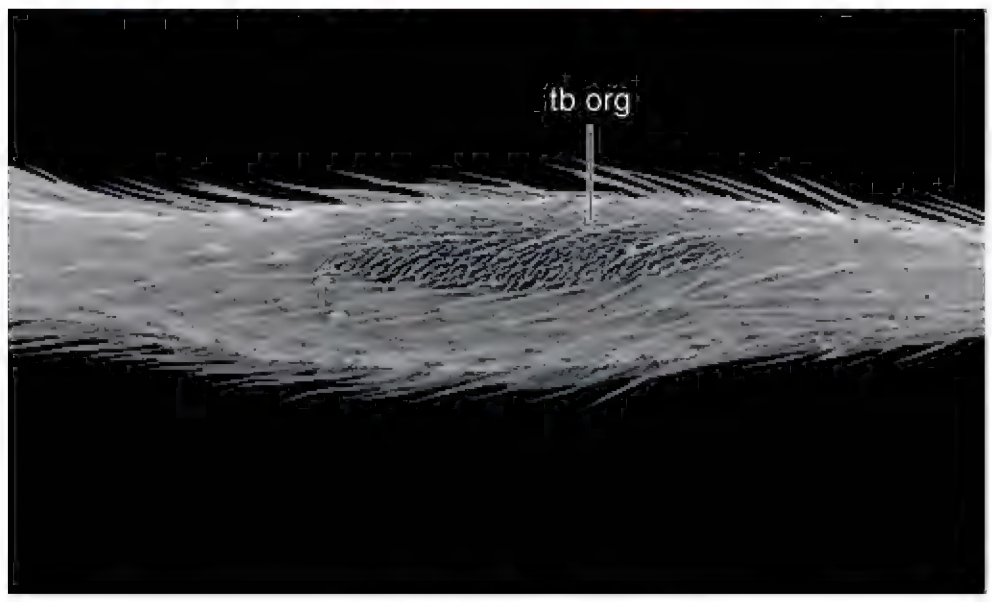


155 *Archimeromyza*

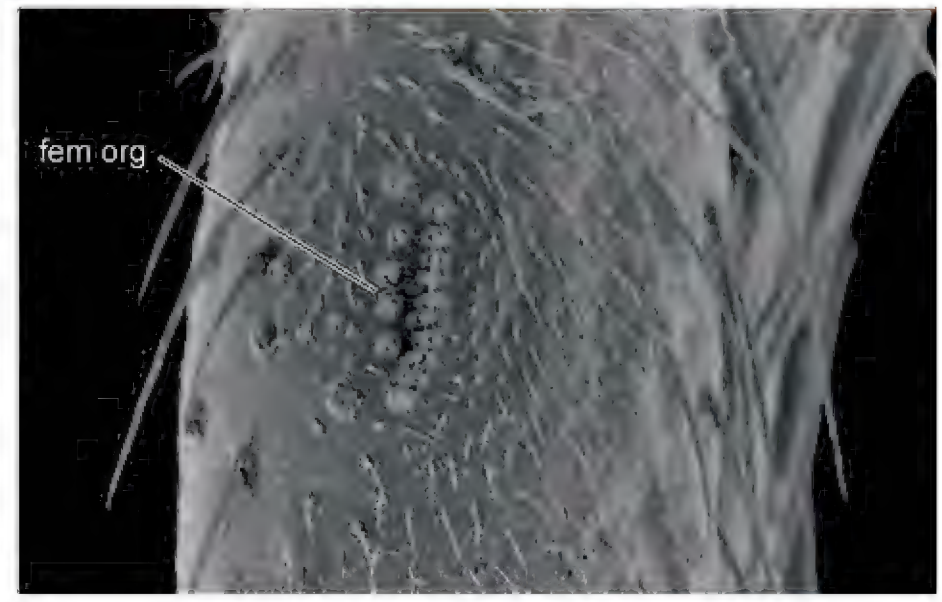
156 *Cadrema*

157 *Epimadiza*

158 *Meromyzella*



159 *Medeventor*



160 *Elachiptera*

Figs 96.154–160. Leg features of Chloropidae: (154) hind leg of *Archimeromyza humeralis* Deeming, lateral view; (155) same; (156) hind leg of *Cadrema* sp., lateral view; (157) fore leg of *Epimadiza* sp., lateral view (non-Afrotropical); (158) hind femur of *Meromyzella capensis* (Loew), lateral view; (159) tibial organ of *Medeventor* sp., dorsal view (non-Afrotropical); (160) femoral organ of *Elachiptera* sp., dorsal view (non-Afrotropical). Fig. 154 (© Trustees of Natural History Museum, London), Fig. 155 (after Deeming 1981a, fig. 18), Figs 159, 160 (© P.R. Riccardi).

Abbreviations: f fem – fore femur; f tb – fore tibia; fem org – femoral organ; h fem – hind femur; h tb – hind tibia; h tb spur – hind tibial spur; sp – spine(s); tb org – tibial organ.

the postpedicel elongate (Fig. 2); eye pubescent; ocellar triangle large, reaching anterior margin of frons; reclinate ocellar setae stout, straight and parallel; postocellar setae slightly reclinate (Fig. 2); scutum and scutellum clothed in very long, irregularly arranged setulae, originating from deep punctures; anepisternum with irregularly arranged setulae, remaining pleural sclerites with irregularly arranged areas of setulae, microtrichia and bare, shiny patches; notopleural setae 1 + 2; and hind tibial spur absent, but with large tibial organ. Deeming (1981*b*) reared *A. punctulatus* (Becker, 1916) from the stems of Poaceae and has described the puparium, including the cephaloskeleton. Adults are attracted to spiders in their webs (Deeming 1981*b*; Ismay 1979), but there is no known direct association with Araneae. Sabrosky (1951: 801) provided an identification key to all species.

Anthracophagella **Andersson** (Chloropinae)**.** A small genus of six valid species (Fig. 30), occurring in the Afrotropical, Australasian and Oriental Regions (Evenhuis & Pape 2020; M. von Tschirnhaus, pers. comm. 2021). One species, *A. politzari* Deeming, 1981, is known from the Afrotropics, recorded from Nigeria (Evenhuis & Pape 2020). The genus is very close to *Chlorops*. Confirmatory characters include: body yellow with black markings (Fig. 30); postpedicel at most 1.25 × as long as deep; arista white (Fig. 30); ocellar triangle large and pruinescent, with 3–4 grooves within and running parallel to lateral margins, only narrow extension of tip reaching anterior margin of frons (Fig. 30); vibrissal angle obtuse and rounded; frontoorbital setae numerous; hind tibial organ absent; and male terminalia with surstylus free from epandrium. The puparium of *A. albovariegata* was described from a specimen developing in the stem of Kodo millet in Madras, India (Deeming 1981a). Deeming (1981a) provided an identification key to world species.

Aphanotrigonum **Duda** (Oscinellinae)**.** A genus of 36 valid species (Figs 31, 32), occurring in the Afrotropical, Australasian, Nearctic, Oriental and Palaearctic Regions (Evenhuis & Pape 2020; M. von Tschirnhaus, pers. comm. 2021). At least one described species, *A. subfasciella* Collin, 1949 (Fig. 32), recorded from Namibia, Nigeria, Oman, United Arab Emirates and Yemen (Deeming & Al-Dhafer 2012; Ismay 2000: 274) and several undescribed species from Namibia and Nigeria, are known from the Afrotropics. Confirmatory characters include: body predominantly black (Figs 31, 32); facial carina low and incomplete, not reaching oral margin (in described Afrotropical species); postocellar setae erect and convergent; anepisternum bare; and hind tibial organ present. The genus can be distinguished from *Conioscinella* as follows: body heavily pruinescent and pleura almost entirely pruinescent; postpronotal setae shorter than notopleural setae (Figs 31, 32); anterior and posterior notopleural setae equally well-developed; scutellum short and broad, with posterior margin straight (in described Afrotropical species) (Fig. 134); apical scutellar setae widely separated and not inserted on tubercles (Fig. 134); and hind tibia with small anteroventral spur, shorter than diameter of tibia (in some Palaearctic species). Larvae of the Palaearctic species, *A. trilineatum* are saprophagous in various cereals and grasses (Ferrar 1987: 110; Wendt 1968). Some larval structures were illustrated by Kreiter (1928) and Nartshuk (1987). There is currently no identification key to the Afrotropical species, but Deeming & Al-Dhafer (2012) provided an identification key to the three species occurring in the Arabian Peninsula.

Apotropina **Hendel** (Siphonellopsinae)**.** A genus of 82 valid species (Fig. 33), occurring in all zoogeographical regions, except Antarctica (Evenhuis & Pape 2020; M. von Tschirnhaus, pers. comm. 2021). The genus is most speciose in the Southern Hemisphere. The eight Afrotropical species are distributed in the Atlantic Ocean Islands, Central and East Africa, the Indian Ocean Islands, Southern Africa, Southern Arabian Peninsula and West Africa (Deeming & Al-Dhafer 2012; Sabrosky 1982) and additional undescribed species are known from Namibia and Zimbabwe (Sabrosky 1982). Confirmatory characters include: usually having three fronto-orbital setae, usually long, with the anterior sometimes lateroclinate; proclinate and divergent ocellar setae; and two long, strong postpronotal setae, with the inner one inclinate and the outer one reclinate. Species are unusually setose among chloropids and many have more than one pair of dorsocentral setae and the hind tibia has a small anteroventral comb. The biology and immature stages remain unknown, although extralimital species have been reared from nests of aculeate Hymenoptera and the nest of a gannet in New Zealand (Ferrar 1987: 117). Although *Apotropina* occurs in a wide variety of habitats, it is most often associated with water bodies, such as river margins inland and seashores. Adults have been found aggregating in large numbers in rock shelters and domestic dwellings (Kirk-Spriggs *et al*. 2001), under an overhanging rock in Australia in 2002 (M. von Tschirnhaus, pers. comm. 2020) or on branches overhanging a river in Papua New Guinea (J.W. Ismay, pers. obs.). In Europe, adults aggregate on the ball-shaped accumulations of dead females of *Atherix ibis* (F., 1798) (Athericidae) overhanging water courses in which the hatched Ibis fly larvae feed on their collective mothers before dropping into the water (Tschirnhaus 2021). An identification key to the nine Afrotropical species was provided by Sabrosky (1982).

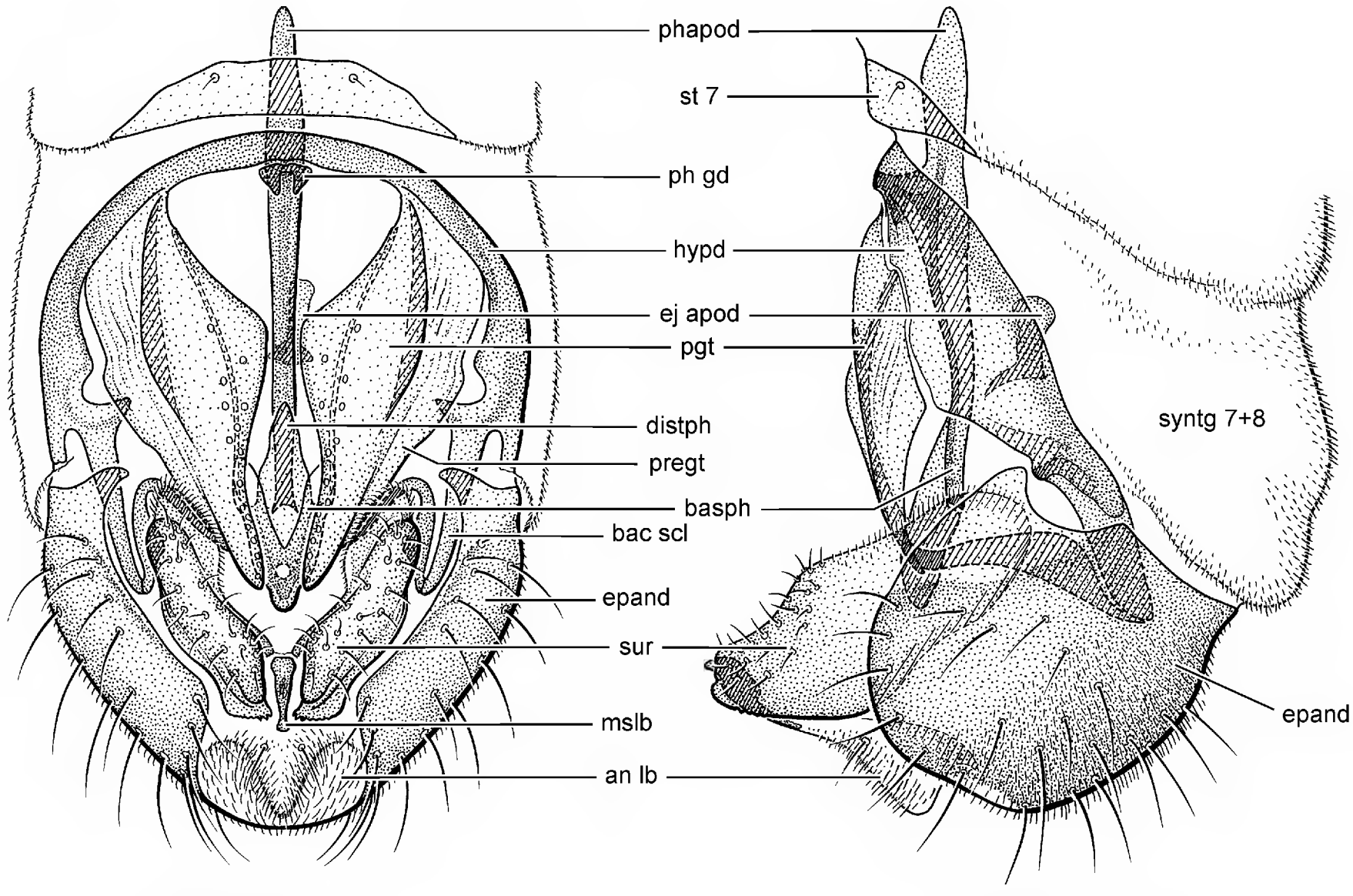
Archimeromyza **Deeming** (Chloropinae)**.** An endemic monotypic genus, with the single species, *A. humeralis* Deeming, 1981 (Fig. 34), recorded from South Africa (Evenhuis & Pape 2020). Confirmatory characters include: body yellow with black markings (Fig. 34); frons with anterior margin scarcely extended beyond anterior margin of eye; ocellar triangle large, with setulae within lateral margin; parafacial narrow (not visible in lateral view); notopleural setae 1 + 2; hind femur thickened, more than twice as broad as tibia, thicker than at least one other femur; tibia correspondingly curved (Figs 154, 155); and indistinct narrow tibial organ present. This genus is closely related to *Meromyza*, but differs in the irregular anteroventral row of broad, thick spines on the apical half of the hind femur (Figs 154, 155) and the male postgonites are not enlarged and not projecting as in *Meromyza*. The biology and immature stages of the species remain unknown.

Arcuator Sabrosky (Oscinellinae)**.** A genus of 16 small, predominantly yellow valid species (Fig. 35), occurring in the Afrotropical, Australasian, Oriental and Palaearctic Regions (Evenhuis & Pape 2020). Ten species are recorded from the Afrotropics, distributed in Central and East Africa, Indian Ocean Islands, Southern Africa, Southern Arabian Peninsula and West Africa (Deeming & Al-Dhafer 2012; Evenhuis & Pape 2020; Sabrosky 1985). Two undescribed species are known from Ghana, Namibia, Madagascar, South Africa and Uganda (Sabrosky 1985). *Arcuator* belongs to a group of Oscinellinae in which the hind tibia bears a distinct apical spur, but in at least one species the spur may be poorly developed.

Confirmatory characters include: body yellow (Fig. 35); ocellar triangle small, reaching (at most), half-length of frons; ocellar setae erect and cruciate; fronto-orbital setae 4–7, erect, slightly reclinate; postocellar setae cruciate; pleura partly shiny; anepisternum bare, often with black macula on ventral part (Fig. 35); scutellum shorter than wide, usually broadly rounded in outline; apical scutellar setae usually widely separated basally, with 1–2 pairs of lateral setae; wing with apical section of vein M_1 curving first towards vein R_{4+5}, then away from it (Fig. 140); and cells r_1 and r_{2+3} subequal in width (Fig. 140). The biology and immature stages remain unknown, although adults have been recorded as attracted to honeydew (Sabrosky 1985) or were observed in South Africa as pollinators (M. von Tschirnhaus, pers. comm. 2021). Sabrosky (1985) revised the genus and provided an identification key to Afrotropical and Palaearctic species.

***Assuania* Becker** (Chloropinae)**.** A genus of seven valid species (Figs 36, 111), occurring in the Afrotropical, Oriental and Palaearctic Regions (Evenhuis & Pape 2020; M. von Tschirnhaus, pers. comm. 2021). Five species occur in the Afrotropics, distributed in East and Southern Africa (Evenhuis & Pape 2020). The Palaearctic species, *A. thalhammeri* (Strobl, 1893), recorded from Algeria and Egypt, may be recorded from the Afrotropics in the future. Deeming and Al-Dhafer (2012) recorded an *Assuania* sp. nr *thalhammeri* (Strobl, 1893) from Yemen. Confirmatory characters include: antennal postpedicel at least 1.5 × as long as deep (Fig. 36); arista black, slender and virtually bare (Fig. 36); ocellar triangle large, almost reaching anterior margin of frons (Fig. 111); scutum more or less shiny black (Figs 36, 111); apical scutellar setae not closely approximated; wing crossveins *dm–m* and *r–m* separated by distance much more than length of crossvein *dm–m* (Fig. 36); tibial organ absent; and male terminalia similar to *Lagaroceras*. It has been reared in India from the furled leaves of bananas (Ferrar 1987: 115), but the immature stages remain unknown. No identification key to species is currently available.

***Bathyparia* Lamb** (Chloropinae)**.** An endemic monotypic genus, with the single described species, *B. praeclara* Lamb, 1917 (Fig. 37), recorded from Madagascar, South Africa and Tanzania (Evenhuis & Pape 2020). Cherian & George (2013) considered *Bathyparia* a synonym of *Cerais* Wulp, but this was not followed by Riccardi & Amorim (2020) and *Bathyparia* is here retained as a separate genus. *Bathyparia praeclara* is similar to the genus *Eutropha*. Confirmatory characters include:



161 *Chlorops* ♂ 162 *Chlorops* ♂

Figs 96.161–162. Male postabdomen of Chloropidae: (161) *Chlorops rubicundus* Adams, ventral view (non-Afrotropical); (162) same, lateral view. Figs 161, 162 (Sabrosky 1987, figs 65, 66).

Abbreviations: an lb – anal lobe: bac scl – bacilliform sclerite; basph – basiphallus; distph – distiphallus; ej apod – ejaculatory apodeme; epand – epandrium; hypd – hypandrium; mslb – mesolobus (fused cerci); pgt – postgonite; ph gd – phallic guide; phapod – phallapodeme; pregt – pregonite; st – sternite; sur – surstylus; syntg – syntergite.

head, thorax and abdomen almost entirely clothed in brilliant, silvery white setulae (lacking black setula) (Fig. 37); postpedicel at least 1.5 × as long as deep; arista not thickened (Fig. 37); ocellar triangle only extending to *ca* half-length of frons and in width occupying only middle half of frons; gena less than 0.4 depth of eye; anepisternum with long (not exceeding diameter of postpedicel) silvery white, reflective setulae over entire surface (Fig. 37); scutellum without closely approximated apical setae; wing cell r_1 at apex of vein R_1, not narrower than cell r_{2+3}; crossveins *dm–m* and *r–m* separated by distance much greater than length of crossvein *dm–m* (Fig. 37); and distinct hind tibial organ present. The biology and immature stages remain unknown, although the species is usually found close to the sea.

***Cadrema* Walker** (Oscinellinae)**.** A genus of 47 valid species (Fig. 38), occurring in all zoogeographical regions, except Antarctica (Dawah *et al*. 2020; Evenhuis & Pape 2020; M. von Tschirnhaus, pers. comm. 2021; Nartshuk 2002, 2010*a*). Eight species are recorded from the Afrotropics (Deeming & Al-Dhafer 2012; Evenhuis & Pape 2020), distributed in Atlantic Ocean Islands, Central and East Africa, Indian Ocean Islands, Southern Africa and the Southern Arabian Peninsula (Dawah *et al*. 2020; Evenhuis & Pape 2020). Confirmatory characters include: postpedicel reniform (Fig. 38); ocellar triangle shiny; ocellar setae and larger postocellar setae erect and cruciate; anepisternum bare; katepisternum with long dorsal posterior seta, latero-clinate and proclinate (Fig. 130); wing vein M_1 straight (Fig. 38); and hind tibia (in most species), with strong preapical or antero-ventral spur equal to, or longer than, diameter of tibia (Fig. 156) and tibial organ. Several species in the genus have been reared in the Australasian and Oceanian Regions from decaying plant tissue and decaying animals, including Mollusca, pig dung, cotton bolls and decaying marine animals (Bezzi 1928: 150; Ferrar 1987: 110; Nartshuk 2010*a*). Nartshuk (2010*a*) recorded *C. minor* as being reared from *Capsicum* in Malaysia and from rotting coconuts in Seychelles. *Cadrema pallida* has also been reared from honeydew on leaves of *Ficus* in Seychelles (J.C. Deeming, unpubl.). The puparium was described by Bohart & Gressitt (1951). An identification key to species of the Indian Ocean Islands and coastline was published by Nartshuk (2002), which includes all Afrotropical species.

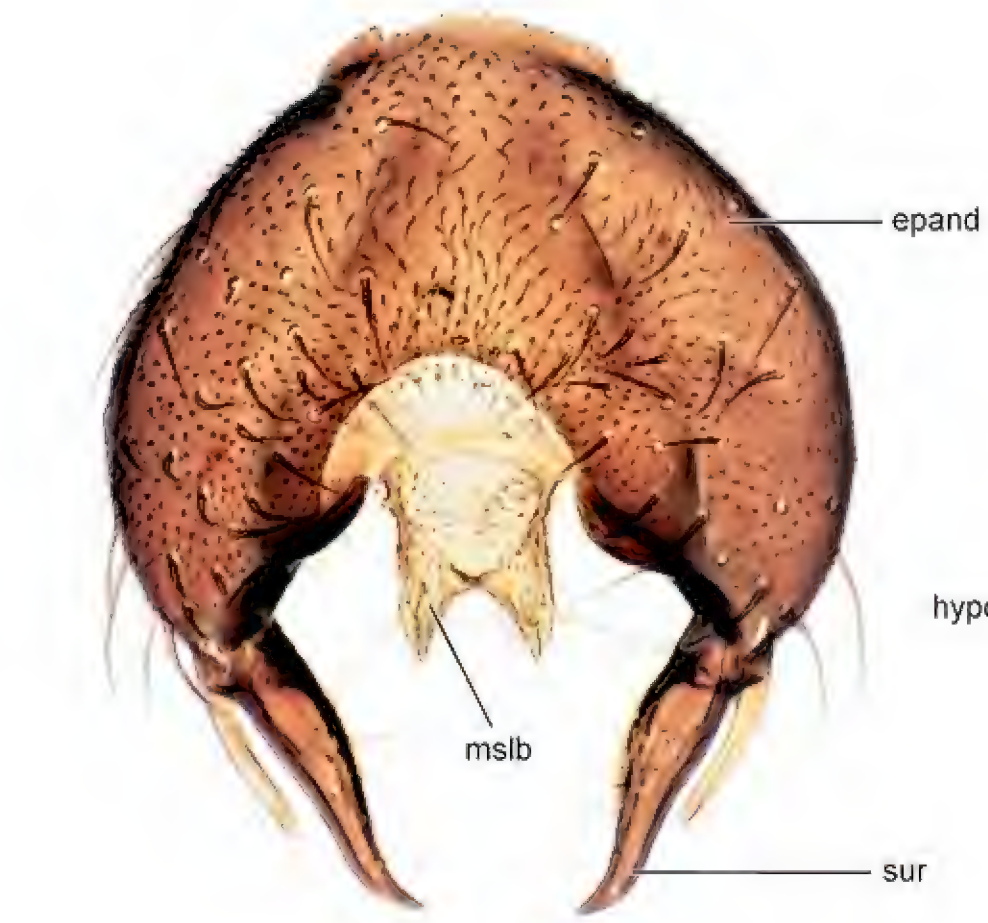
***Calamoncosis* Enderlein** (Oscinellinae)**.** A genus of 45 valid species (Fig. 39), occurring in all zoogeographical regions, except Antarctica (Evenhuis & Pape 2020; M. von Tschirnhaus, pers. comm. 2021). Four species are recorded from the Afrotropics: *C. abbreviata* Deeming, 2011, described from Botswana and United Arab Emirates; *C. aenescens* (Becker, 1916), recorded from Ethiopia, Kenya, Mozambique, Namibia, Uganda and Yemen (Deeming & Al-Dhafer 2012); *C. pauliani* Séguy, 1953, described from Madagascar; and *C. sorghivora* described from Yemen and including the puparium and cephaloskeleton as it was reared from Sorghum. Confirmatory characters include: eye densely pubescent; ocellar triangle moderate to large, with numerous strong piliferous punctures and setulae within lateral margin; ocellar and postocellar setae reclinate and parallel; anepisternum bare (Fig. 39); hind tibia without apical or subapical spur, but with well-developed, oval tibial organ; and mid femoral organ present, with large and numerous "warts". The genus has been reared from plant tissue of *Glyceria*, *Phalaris*, *Phragmites* and *Stipa* in the Palaearctic and as an inquiline from plant tissue of *Phragmites* damaged by other insects (Collin 1946; Ferrar 1987: 110). Grochowska provided detailed descriptions of all immature stages of the non-Afrotropical species *C. apricа* (Grochowska 2002), while Deeming & Al-Dhafer (2012) commented that *Calamoncosis* species attack Sorghum under water-stress in the Afrotropical Region. Deeming & Al-Dhafer (2012) provided an identification key to *C. aenescens* and *C. sorghivora*.

***Camarota* Meigen** (Chloropinae)**.** A genus of six valid species (Figs 40–42), occurring in the Afrotropical, Oriental and Palaearctic Regions (Evenhuis & Pape 2020; Riccardi & Tschirnhaus 2018). Three species are recorded from the Afrotropics: the widespread *C. angustifrons* Bezzi, 1908 (Fig. 40), recorded from Burundi, Eritrea, Kenya, Mozambique, South Africa, Tanzania and Uganda (Evenhuis & Pape 2020); *C. cylindrica* (Fig. 42), recorded from Cameroon, Mozambique, Nigeria, Rwanda, South Africa and Uganda; and *C. ugandae* Riccardi & Tschirnhaus, 2018, described from Uganda. *Camarota curvipennis* (Fig. 41) was also recorded from an area of Saudi Arabia close to the border of Yemen (Dawah *et al*. 2020). *Camarota angustifrons*, *C. curvipennis* and *C. ugandae* are beetle-like in appearance and fold their wings against the abdomen, whereas *C. angustifrons* has retained some of the less derived characters. Species in this genus have very similar male terminalia and share characters in the immature stages (Deeming 1981*a*). Confirmatory characters include: arista thickened, flattened and blade-like and uniquely within all Chloropidae with a dark transverse band at the base of the arista (Riccardi & Tschirnhaus 2018) (Figs 4, 40–42); head depressed, much longer than high; eye with long axis virtually horizontal (Figs 40–42); frons with anterior margin projecting (Fig. 4); ocellar triangle large, reaching (or almost reaching) anterior margin of frons, with line of setulae within lateral margin (Fig. 4); scutum strongly punctate; anepisternum with numerous setulae; wing vein R_{2+3} fused with, or is in contact with, vein R_1; costal vein (C) running very close to R_1 throughout its length (Figs 40–42); auxiliary vein present between veins M_1 and M_4 (Fig. 42); and narrow tibial organ present on hind tibia. *Camarota angustifrons* has been reared from grasses, *C. cylindrica* from rice (Deeming 1981*a*) and *C. curvipennis* from Barley, Maize, Oats, Rye, Wheat and grasses in Europe (Riccardi & Tschirnhaus 2018). Balachowsky & Mesnil (1935) figured the larva of *C. curvipennis*. Deeming (1981*a*) figured part of the puparium of *C. cylindrica* and described and figured the puparium and the cephaloskeleton of *C. angustifrons*. Riccardi & Tschirnhaus (2018) provided an identification key to all known species.

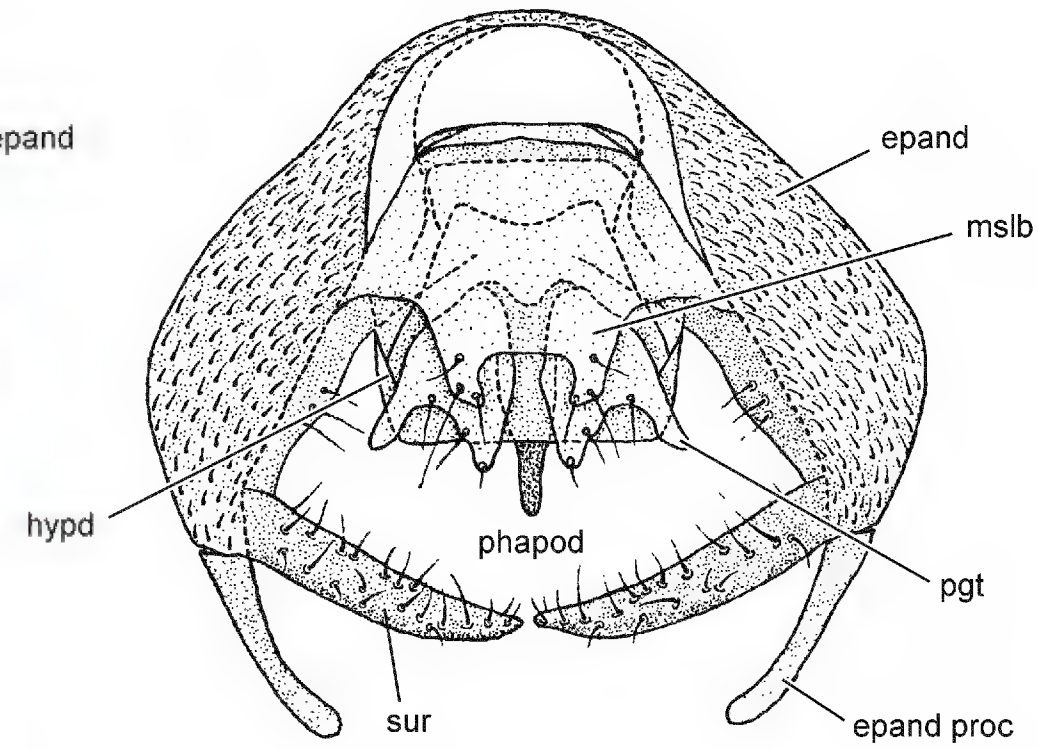
***Camptoscinella* Sabrosky** (Oscinellinae)**.** An endemic genus of two described species (Fig. 43): *C. annulitibia* Sabrosky, 1951, described from Uganda; and *C. insulicola* Bezzi, 1926, described from Rodrigues Is. in the Indian Ocean (Evenhuis & Pape 2020). There is an additional undescribed species known from Kenya. Confirmatory characters include: postpedicel slightly oval; arista pubescent (Fig. 43); eye microscopically pubescent; ocellar triangle short to medium, dull and distinctly pruinescent; gena narrow; facial carina absent; ocellar and postocellar setae short, erect and convergent; fronto-orbital setae thin and evenly sized; scutum pruinescent; pleura partly shiny; anepisternum bare; notopleural setae 1 + 2; scutellum very short, apically rounded, with disc convex; scutellar setae not on tubercles, with one pair of apical scutellar setae and one pair of lateral scutellar setae; wing with first costal sector, longer than second; crossvein

r–m positioned at close to half-length of wing (an unusually wide gap in costagial break); vein R_1 weakened close to costagial break; vein R_{2+3} highly sinuate; vein M_1 straight; crossvein *dm–m* strongly oblique (Fig. 142); and hind tibia without apical or subapical spur, but with large tibial organ. The biology and immature stages remain unknown. The genus and species can be distinguished by reference to Sabrosky (1951: 807).

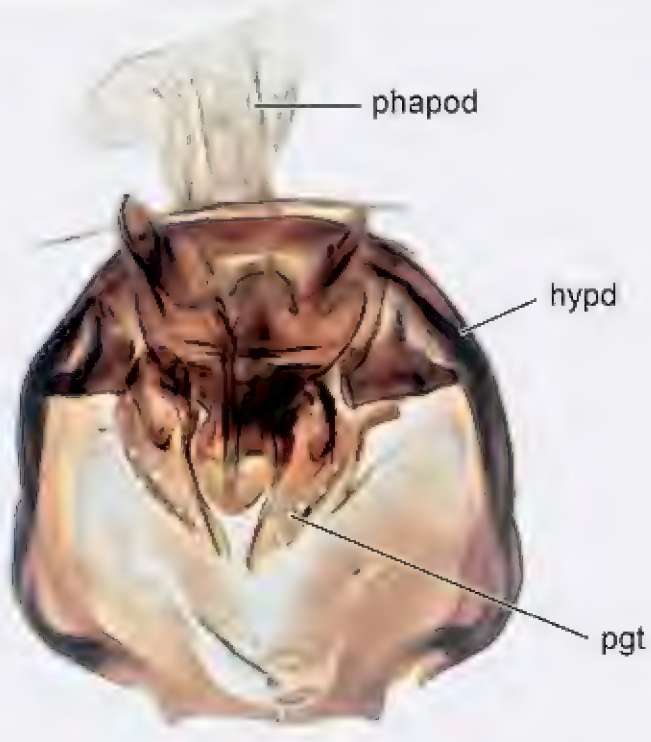
***Caviceps* Malloch** (Oscinellinae)**.** A genus of six valid species (Fig. 44), occurring in the Afrotropical, Australasian and Oriental Regions (Deeming & Al-Dhafer 2012; Evenhuis & Pape 2020; M. von Tschirnhaus, pers. comm. 2021). Only one female specimen of an undetermined species is known from Yemen in the Afrotropical Region (Deeming & Al-Dhafer 2012). Confirmatory characters include: postpedicel short,



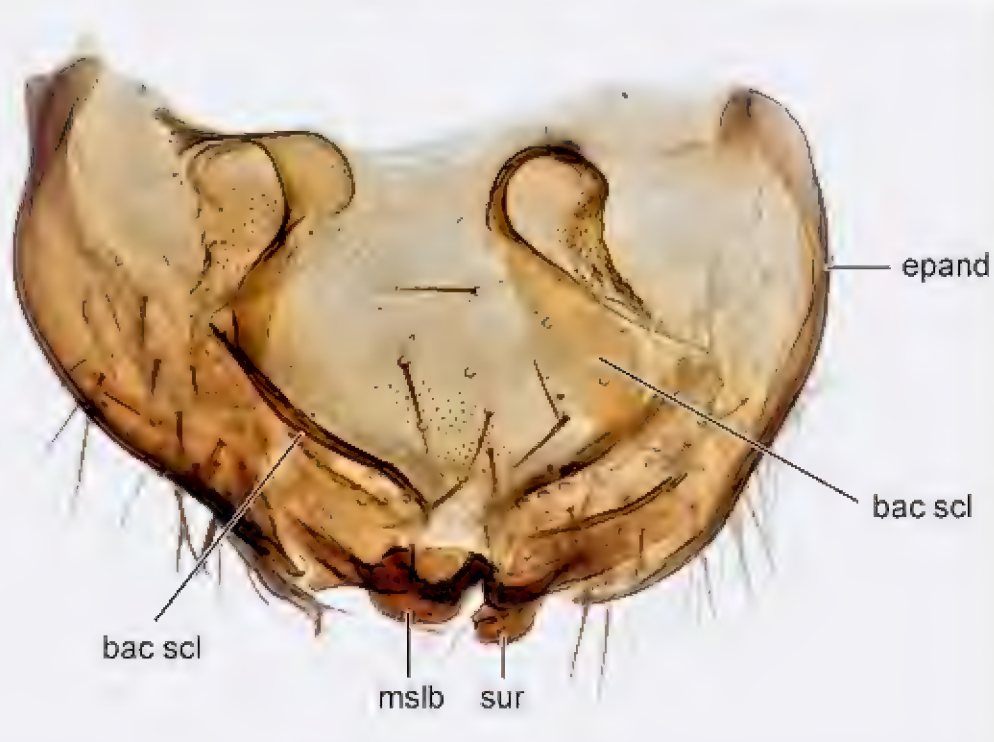
163 *Apotropina* ♂



164 *Apotropina* ♂



165 *Apotropina* ♂



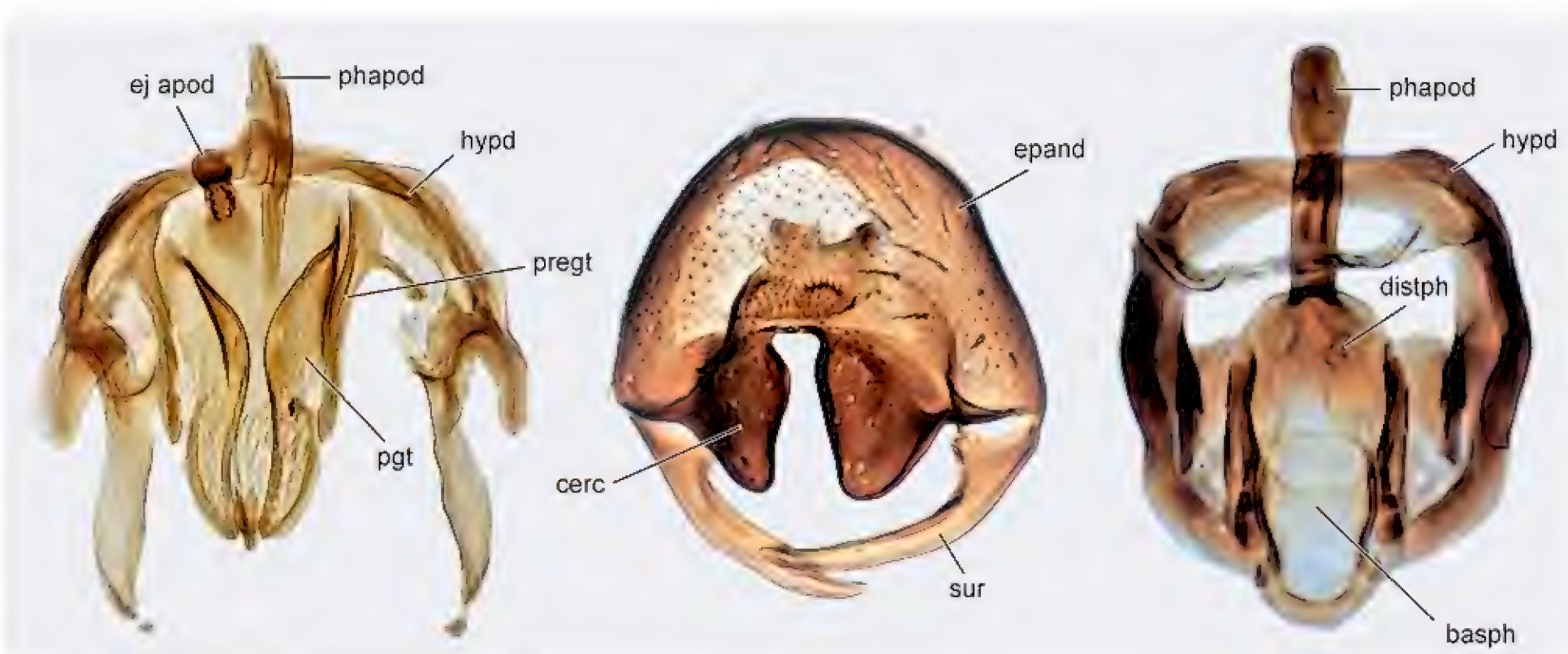
166 *Chlorops* ♂

Figs 96.163–166. Male terminalia of Chloropidae: (163) epandrium of *Apotropina* sp., apical view; (164) *Apotropina gregalis* (Lamb), apical view; (165) hypandrium of *Apotropina* sp. , ventral view; (166) epandrium of *Chlorops* sp., ventral view (non-Afrotropical). Figs 163, 165, 166 (courtesy M.J. Ebejer), Fig. 164 (after Kirk-Spriggs *et al*. 2001*b*, fig. 3).

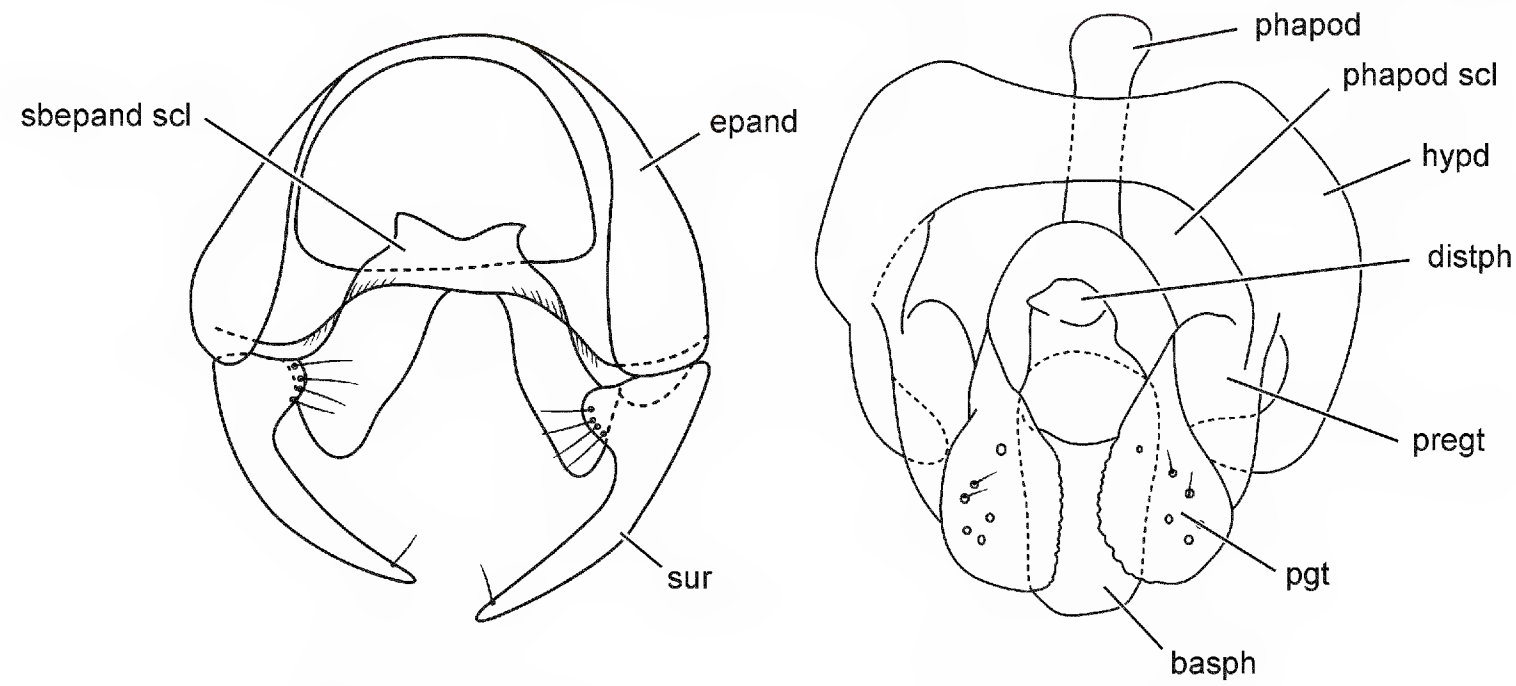
Abbreviations: bac scl – bacilliform sclerite; epand – epandrium; epand proc – epandrial process; hypd – hypandrium; mslb – mesolobus (fused cerci); pgt – postgonite; phapod – phallapodeme; sur – surstylus.

somewhat rounded (Fig. 44); head much deeper than long with gena deep; eye densely setulose; face deeply concave; facial carina triangular in upper part, overhanging face, only developed in dorsal part; ocellar triangle indistinguishable; ocellar setae erect and cruciate; postocellar setae convergent or cruciate; scutum with weakly developed grooves along median and dorsocentral lines; pleura entirely pruinescent; anepisternum bare; scutellum shorter than wide with long apical setae and several short, lateral setae; wing with second costal sector, much longer than third sector; vein R_{2+3} long; anal lobe broad (Fig. 44); and hind tibial spur absent, tibial organ present. The biology and immature stages remain unknown. Kanmiya (1983) provided a description of the genus and included five species, of which *C. huttoni* (Malloch, 1931), has subsequently been transferred to the genus *Aphanotrigonum*.

***Chlorops* Meigen** (Chloropinae)**.** A genus of 343 valid species (Figs 45, 112), occurring in all zoogeographical regions, except Antarctica (Kubík & Barták 2018). Many species described in *Chlorops* have, however, subsequently been transferred to



167 *Chlorops* ♂ 168 *Oscinella* (*Oscinella*) ♂ 169 *Oscinella* (*Oscinella*) ♂



170 *Oscinella* (*Oscinella*) ♂ 171 *Oscinella* (*Oscinella*) ♂

Figs 96.167–171. Male terminalia of Chloropidae (all non- Afrotropical): (167) hypandrium of *Chlorops* sp., ventral view; (168) epandrium of *Oscinella* (*O.*) *frit* (L.), apical view; (169) same, hypandrium, ventral view; (170) same, epandrium, inner view; (171) same, hypandrium, ventral view. Figs 167–169 (courtesy M.J. Ebejer), Figs 170, 171 (after Andersson 1977, figs 61C, 61H).

Abbreviations: basph – basiphallus; cerc – cercus; distph – distiphallus; ej apod – ejaculatory apodeme; epand – epandrium; hypd – hypandrium; pgt – postgonite; phapod – phallapodeme; phapod scl – phallapodemic sclerite; pregt – pregonite; sbepand scl – subepandrial sclerite; sur – surstylus.

other genera, or into new genera and this process is likely to continue. There are 14 species recorded from the Afrotropical Region, distributed in Central, East, Southern and West Africa and the Indian Ocean Islands (Evenhuis & Pape 2020; M. von Tschirnhaus, pers. comm. 2021; authors, pers. obs.). Confirmatory characters include: body yellow with black markings (Figs 45, 112); postpedicel as long as deep; arista black or white (Fig. 45); frons with numerous small frontoorbital setae; ocellar triangle shiny or pruinescent, without setulae or distinct grooves within margins; scutum shiny or strongly pruinescent; vibrissal angle obtuse and rounded (in Afrotropical species); without tibial organ and spur on hind tibia; male terminalia with surstylus free from epandrium; and pre- and postgonites parallel (Figs 161, 162). Larvae are primary stem-borers of grasses and sedges and *C. pumilionis* is a serious pest of cultivated cereals, including Barley and Wheat outside of the region (Nartshuk & Andersson 2013: 179), while some other species are recorded as minor pests (Ferrar 1987: 115). The larvae and/or puparia of five Palaearctic species of *Chlorops* are covered by Balachowsky & Mesnil (1935: 935) and Zhabinskaja (1963) illustrated and described the larvae of further Palaearctic species, but no recent identification key to Afrotropical species is available.

***Chloropsina* Becker** (Chloropinae)**.** A genus of 60 valid species (Fig. 46), occurring in the Afrotropical, Australasian, Oriental and Palaearctic Regions (Deeming & Al-Dhafer 2012; Evenhuis & Pape 2020; M. von Tschirnhaus, pers. comm. 2021). There are 22 species recorded from the Afrotropics distributed in Central, East, Southern and West Africa and the Southern Arabian Peninsula. Two undescribed species are known from Yemen (Deeming & Al-Dhafer 2012). The male terminalia of *Chloropsina* must be dissected to identify this genus with certainty, but it can be distinguished by a pair of band-shaped sclerites lateral to the anus in most species, although it is absent or reduced to setae in a few. The following confirmatory characters can be used as an indication only: postpedicel as long as deep to distinctly longer than deep; arista black or white (Fig. 46); head with all setation present; gena less than 0.5 depth of eye; anepisternum bare; prescutellar dorsocentral seta present; apical scutellar setae not approximated; wing membrane hyaline; cell r_{2+3} at apex of vein R_1, much narrower than cell r_{4+5}; cells *br* and *bm+dm* very narrow (Fig. 46); and hind tibia with distinct organ. The immature stages have been found in *Citrus* roots in Hawaii (Ferrar 1987: 115) and shoots of the grass *Paspalum vaginatum* in Nigeria and the puparium was partially described from the latter locality (Deeming 1981*a*). Deeming (1981*a*) included 20 Afrotropical species and provided an identification key to the then known Afrotropical species and described the puparium and cephaloskeleton of *C. litoralis*. An additional species was added by Deeming & Al-Dhafer (2012) and this paper also included a description of the puparium and the cephaloskeleton of this species.

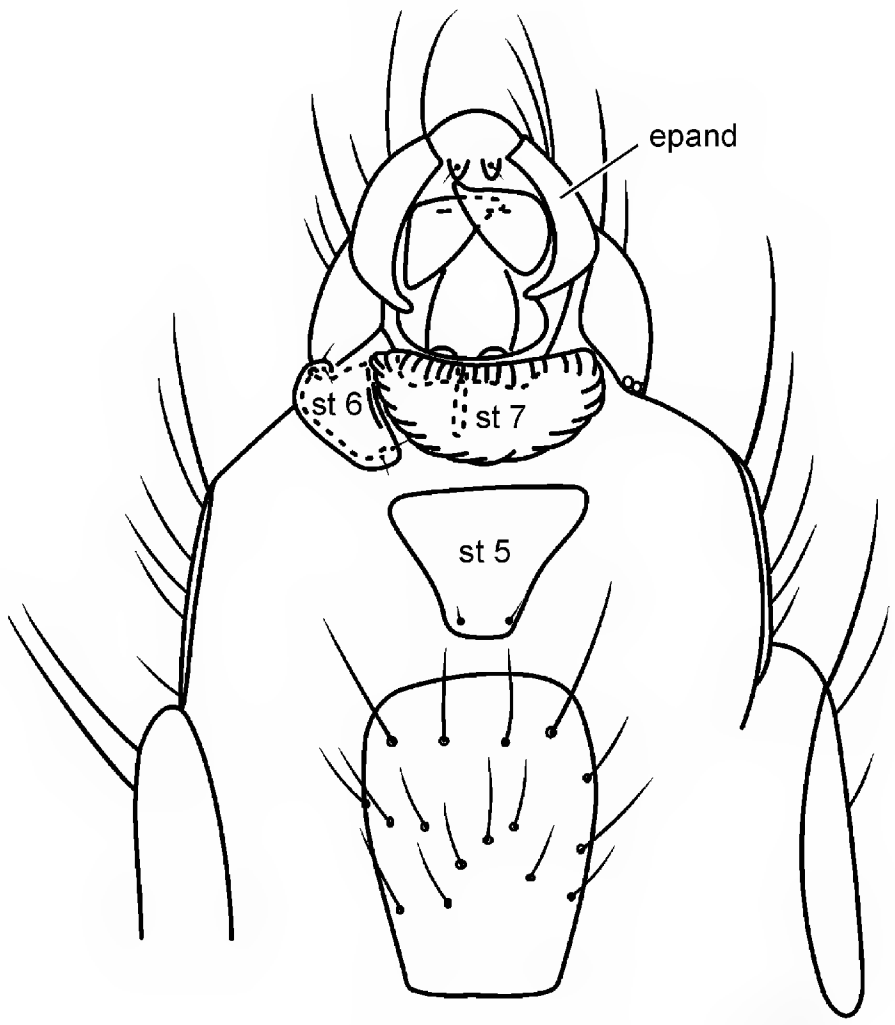
***Chromatopterum* Becker** (Chloropinae)**.** A genus of 20 valid species (Fig. 47), occurring in the Afrotropical, Australasian and Oriental Regions (Evenhuis & Pape 2020; Liu *et al*. 2017*a*; M. von Tschirnhaus, pers. comm. 2021). There are six Afrotropical species (Deeming 1981*a*; Liu *et al*. 2017*a*), distributed in Central, East and West Africa. Confirmatory characters include: arista thin; ocellar triangle large, almost reaching anterior margin of frons; postocellar setae convergent or cruciate; scutum and head black or dark brown, at most with thin light fasciae (Fig. 47); notopleural setae 1 + 2; scutellum wider than long, with apical scutellar setae widely separated; wing membrane (in described Afrotropical species), either distinctly darkened or with wide dark fascia along anterior margin to tip (Fig. 47); hind femur less than twice as broad as tibia (Fig. 47); tibial organ present; and male tergite 5 absent, or only represented by pair of small crescent-shaped sclerites (Fig. 47). The biology of the genus and immature stages remain unknown. Liu *et al*. (2017*a*) provided an identification key to world species, but one undescribed Afrotropical species is known without wing markings and this has been included in the above identification key to genera (P.R. Riccardi, pers. comm. 2021).

***Conioscinella* Duda** (Oscinellinae)**.** A genus of 84 valid species (Fig. 48), occurring in all zoogeographical regions, except Antarctica (Evenhuis & Pape 2020). Eleven species are recorded from the Afrotropical Region, distributed in East Africa, the Indian Ocean Islands and Southern Africa, but there appear to be numerous undescribed species known from throughout the region. *Conioscinella aptera* is a brachypterous species. Species vary in colour, from entirely black to almost entirely yellow. The limits of the genus remain uncertain and several groups have been removed into new genera (*e.g.*, *Arcuator*). It has been used as a "dumping-ground" for species that do not easily fit into other genera and considerable research on the genus on a global basis is required before the taxonomic problems can be resolved. Confirmatory characters include: postpedicel shorter than deep; arista thin (Fig. 6); ocellar triangle usually pruinescent (may be shiny in some species) (Fig. 6); pleura pruinescent in dorsal half or less, but shiny ventrally; wing without elongate vein R_{2+3}; and hind femur not thickened (Fig. 48). Afrotropical species in the genus have been reared from decaying plant material, spider egg masses, grass stems and cereals (Ferrar 1987: 110). Nye (1958) described the immature stages of *C. frontella* and *C. mimula*. There is currently no identification key for Afrotropical species.

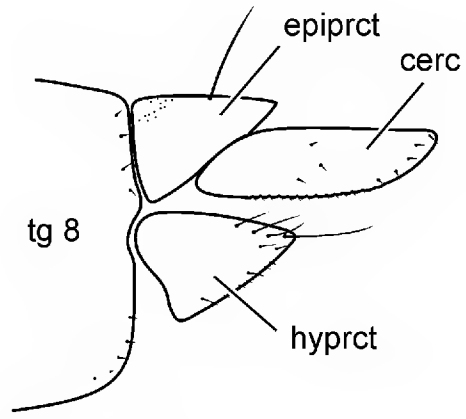
[***Cryptonevra* Lioy** (Chloropinae)**.** A genus of nine valid species (Fig. 49), occurring in the Palaearctic Region (Evenhuis & Pape 2020), including North Africa (Grochowska 2007). There are no confirmed records of the genus from the Afrotropical Region, but it is known very close to the border and is included here for completeness. Confirmatory characters include: body mostly black with yellow tarsi (Fig. 49); postpedicel *ca* as long as deep, slightly pointed anterodorsally; arista not thickened, but with fine pubescence (Fig. 49); ocellar triangle large, dulled by micro-sculpture, with row of setulae within lateral margins; scutum not strongly convex (Fig. 49); with distinct setulae on scutum and scutellum; wing membrane hyaline (Fig. 49); male mid femur with distinct femoral organ, the only genus of Chloropinae with this character; and hind tibia of both sexes with distinct tibial organ. The immature stages of some species are known to be associated with Common reed and particularly as inquilines with *Lipara* galls in reed in the Holarctic Region. Grochowska (2007) provided an identification key to the adults of Palaearctic species associated with reed. Grochowska provided detailed descriptions of all immature stages of the non-Afrotropical species *C. diadema* (Grochowska 2008*b*), *C. flavitarsis* (Grochowska 2008*c*) and *C. nigritarsis* (Grochowska 2007*b*). Nartshuk & Andersson (2013: 186) provided a description of the genus, an identification key to the known third-instar

larvae and to Fennoscandian species, together with descriptions of several species.]

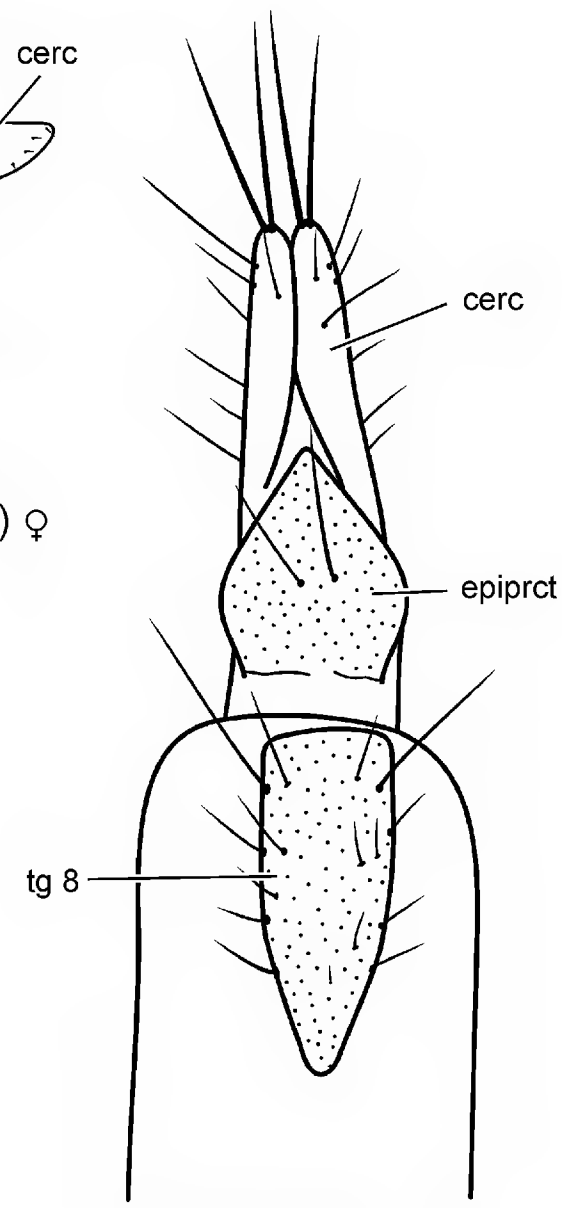
***Dactylothyrea* de Meijere** (Oscinellinae)**.** A genus of 14 valid species (Fig. 113), occurring in the Afrotropical and Oriental Regions (Evenhuis & Pape 2020). Seven species are known from the Afrotropics distributed in Central, East and West Africa and the Indian Ocean Islands (Evenhuis & Pape 2020). Confirmatory characters include: arista distinctly pubescent (sometimes microscopically); eye large and bare, with long axis vertical; gena linear; ocellar setae proclinate and divergent; postocellar setae cruciate; scutum shiny, black, but densely and coarsely rugose (Fig. 113); anepisternum setulose; one presutural supra-alar seta present, but without anterior and one posterior notopleural seta; scutellum with 2–3 pairs of elongate, finger-like projections (Fig. 113), each much longer



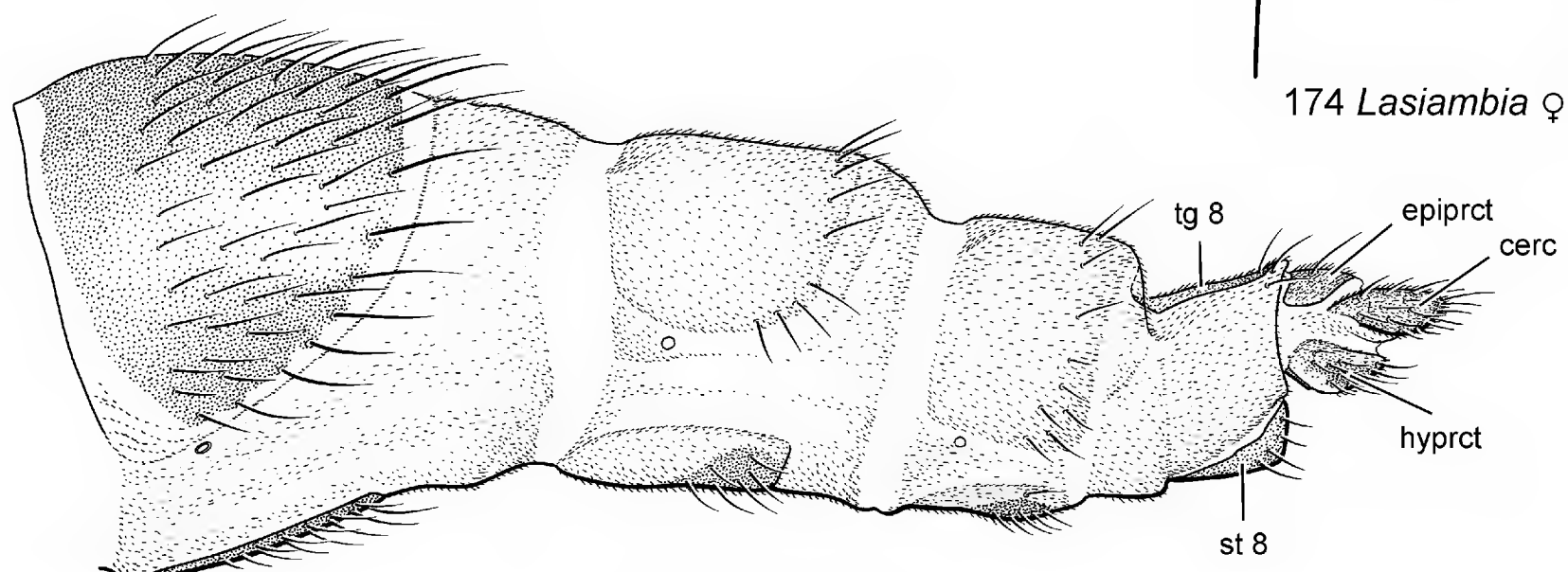
172 *Apotropina* ♂



173 *Diplotoxa* (*Pseudopachychaeta*) ♀



174 *Lasiambia* ♀



175 *Chlorops* ♀

Figs 96.172–175. Male abdomen and female abdomen and terminalia of Chloropidae (all non-Afrotropical): (172) male abdomen of *Apotropina longepilosa* (Strobl), ventral view; (173) apex of blade-like female ovipositor of *Diplotoxa* (*Pseudopachychaeta*) *oscinina* (Fallén), lateral view; (174) same, *Lasiambia brevibucca* (Duda), dorsal view; (175) female abdomen of *Chlorops rubicundus* Adams, lateral view. Figs 172, 174 (after Andersson 1977, figs 21A, 50E, respectively), Fig. 173 (after Ismay 1978, fig. 377), Fig. 175 (Sabrosky 1987, fig. 67).

Abbreviations: cerc – cercus; epand – epandrium; epiprct – epiproct; hyprct – hypoproct; st – sternite; tg – tergite.

than broad (from almost as long to longer than scutellum), bearing scutellar setae; and hind tibial organ absent. The biology and immature stages remain unknown. Sabrosky (1979: 318) provided an identification key to Afrotropical species.

***Dicraeus* Loew** (Oscinellinae)**.** A genus of 72 valid species (Fig. 50), occurring in all zoogeographical regions, except the Neotropical Region and Antarctica (Deeming 1979; Evenhuis & Pape 2020; Liu *at al*. 2019; M. von Tschirnhaus, pers. comm. 2021). Six species are recorded from the Afrotropical Region, distributed in Atlantic Ocean Islands, East, Southern and West Africa. Confirmatory characters include: antenna not elongate, with arista thin; ocellar triangle smooth, without rows of punctures and pruinescent; facial carina absent; ocellar setae erect to slightly reclinate; fronto-orbital setae fine and evenly sized, the most posterior slightly larger than remainder; postocellar setae cruciate; pleura extensively shiny, at least anepisternum, anepimeron, or katepisternum with extensive shiny areas (Fig. 50); anepisternum bare; notopleural setae 1 + 1 or 1 + 2; scutellum shorter than wide and usually broadly rounded in outline, without finger-like projections or distinct tubercles; apical scutellar setae widely separated basally, with one or two pairs of lateral setae; wing with second costal sector 2.5 × as long as the third costal sector; vein R_1 parallel to vein R_{2+3} for most of its length (Fig. 50); hind tibia without apical or subapical spur, but with tibial organ; and males with femoral organ on mid femur. In the Palaearctic, larvae occur in the seed heads of grasses and destroy the developing seeds (Ferrar 1987: 111) at the milky grain stage and is regarded as a minor pest species. In West Africa, Deeming (1979) recorded *D. pennisetivora* feeding on the millet *Pennisetum glaucum* causing extensive damage. Deeming (1979) revised the Afrotropical species, illustrated relevant adult morphological characters of the six species and the third-instar larva and puparium of *D. pennisetivora* and provided an identification key.

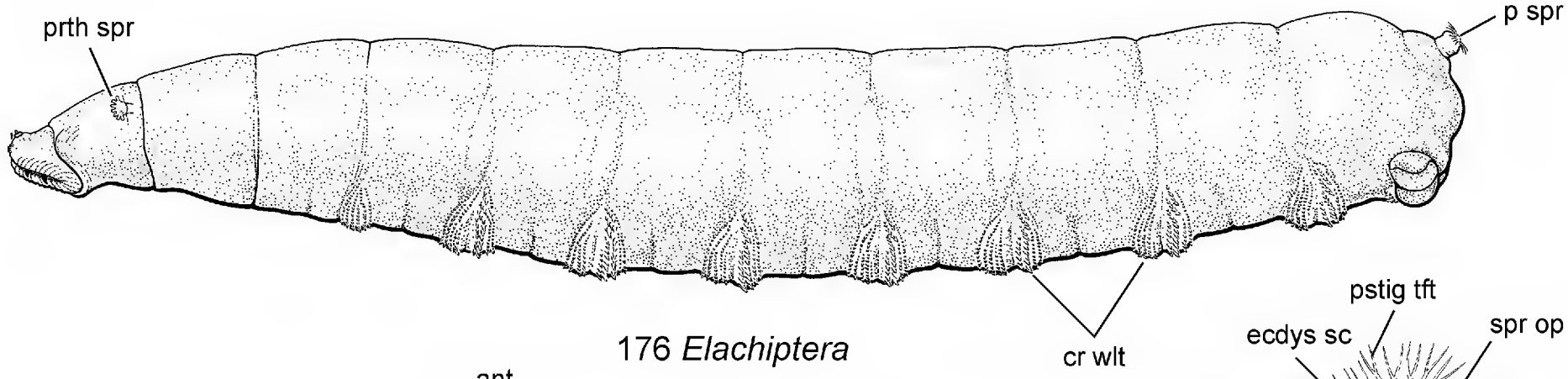
***Diplotoxa* Loew** (Chloropinae)**.** A genus of 48 valid species (Figs 51, 53, 89), occurring in all zoogeographical regions, except Antarctica (Evenhuis & Pape 2020). In agreement with Spencer (1986), Wheeler (2010: 1149) and Wheeler & Forrest (2003), *Elliponeura* and *Pseudopachychaeta* are here treated as subgenera of *Diplotoxa*, along with *Diplotoxa sensu stricto*. Nartshuk (2012) and Riccardi & Amorim (2020) retain these as separate genera, but the latter pointed out that further work is needed to establish the generic limits. Confirmatory characters include: arista short-pubescent, not thickened and flattened or blade-like (Figs 51, 53, 89); large ocellar triangle pruinescent or shiny; wing membrane hyaline; crossveins *r–m* and *dm–m* closely approximated, separated by distance less than length of *dm–m* (Figs 51, 143); and posterior femur less than twice as broad as tibia. *Diplotoxa sensu stricto* comprises 16 species (Figs 51, 143) (Evenhuis & Pape 2020). The subgenus is not formally recorded from the Afrotropics. Subgeneric characters are as for *Diplotoxa sensu lato* above, but the ocellar triangle is shiny and wing crossvein *dm–m* is present (Fig. 51). *Diplotoxa* (*Elliponeura*) (Fig. 53), comprised five species (Evenhuis & Pape 2020). The subgenus is not formally recorded from the Afrotropics, but several undescribed species are known from Nigeria and Mauritius (J.C. Deeming, unpubl. & J.W. Ismay, unpubl.). Subgeneric characters are wing crossvein *dm–m* absent and species are mainly yellow (Fig. 53), otherwise the characters are as for *Diplotoxa sensu lato* above. *Diplotoxa* (*Pseudopachychaeta*) comprised 27 species (Fig. 89) (Evenhuis & Pape 2020), with one species, *D.* (*P.*) *rectinervis* (Becker, 1912), described from Ethiopia in the Afrotropics. One undescribed species is known from Nigeria (J.C. Deeming, unpubl.). Subgeneric characters are as for *Diplotoxa sensu lato* above, but the ocellar triangle is pruinescent. Extralimital species of *Diplotoxa sensu stricto* have been reared from the seed heads of sedges, several *Eleocharis* and larvae have been discovered (Ferrar 1987: 115; Valley *et al*. 1969). The Nearctic species *D.* (*E.*) *debilis* is also known to be a primary invader of inflorescences of *Eleocharis* (Ferrar 1987: 115; Valley *et al*. 1969). The immature stages of extralimital species of *Diplotoxa* (*Pseudopachychaeta*) are further known to develop in seed heads of Cyperaceae and are phytophagous (Nartshuk & Andersson 2013: 223) and Nartshuk (1987) illustrated the puparium (p. 91) and the cephaloskeleton (p. 99) of the Palaearctic *D.* (*P.*) *ruficeps*. The writers have reared the same species from the seed heads of *Eriophorum* species. No identification key to Afrotropical species is currently available.

***Elachiptera* Macquart** (Oscinellinae)**.** A genus of 91 valid species (Fig. 114), occurring in all zoogeographical regions, except Antarctica (Tschirnhaus 2017). Twenty-one species are recorded from the Afrotropics, distributed in Atlantic Ocean Islands, Central and East Africa, Indian Ocean Islands, Southern, West Africa and Southern Arabian Peninsula (Deeming & Al-Dhafer 2012; Evenhuis & Pape 2020; Tschirnhaus 2017), these include the former genus *Cyrtomomyia* Becker that was synonymised with *Elachiptera* by Mlynarek & Wheeler (2018), but all literature is still under *Cyrtomomyia*. Confirmatory characters include: arista thickened and blade-like, with long pubescence (Figs 7, 114); ocellar triangle smooth, without rows of punctures (Fig. 7); facial carina absent; ocellar setae erect to slightly reclinate; postocellar setae erect and convergent or cruciate; 1–2 pairs of fronto-orbital setae longer compared to the remainder (Figs 7, 114), in the former *Cyrtomomyia* all fronto-orbital setae are even in size; scutum with three weakly incised lines of punctures, but not deeply grooved; pleura extensively shiny, at least the anepisternum, anepimeron or katepisternum, with extensive shiny areas; anepisternum bare; scutellum usually slightly to strongly elongate, thin and flattened, with surface rugose, trapezoidal in outline, apically subtruncate, with 1–3 pairs of setae, which may be on enlarged tubercles or finger-like projections (Fig. 114); femoral organ on mid femur (Fig. 160) and tibial organ on hind tibia present; and weak spur, equal to diameter of tibia, present on hind tibia in one species (*E. acanthellata*). One undescribed Afrotropical species from Mt Kilimanjaro, Tanzania is brachypterous (Nartshuk & Tschirnhaus 2012). Extralimital species of *Elachiptera* are well-known as invaders of plant tissue damaged by other organisms (Ferrar 1987: 111) and *E. occipitalis* has been reared from Sorghum shoots in the Afrotropics (J.C. Deeming, unpubl.). Ferrar (1987: 618, 119) includes figures of the cephaloskeleton and the prothoracic spiracle of an *Elachiptera* species. Immature stages (Figs 176, 178–181) were described by Sabrosky (1987: 1063). Sabrosky (1951: 782) provided an identification key to most Afrotropical species, except for the few described more recently.

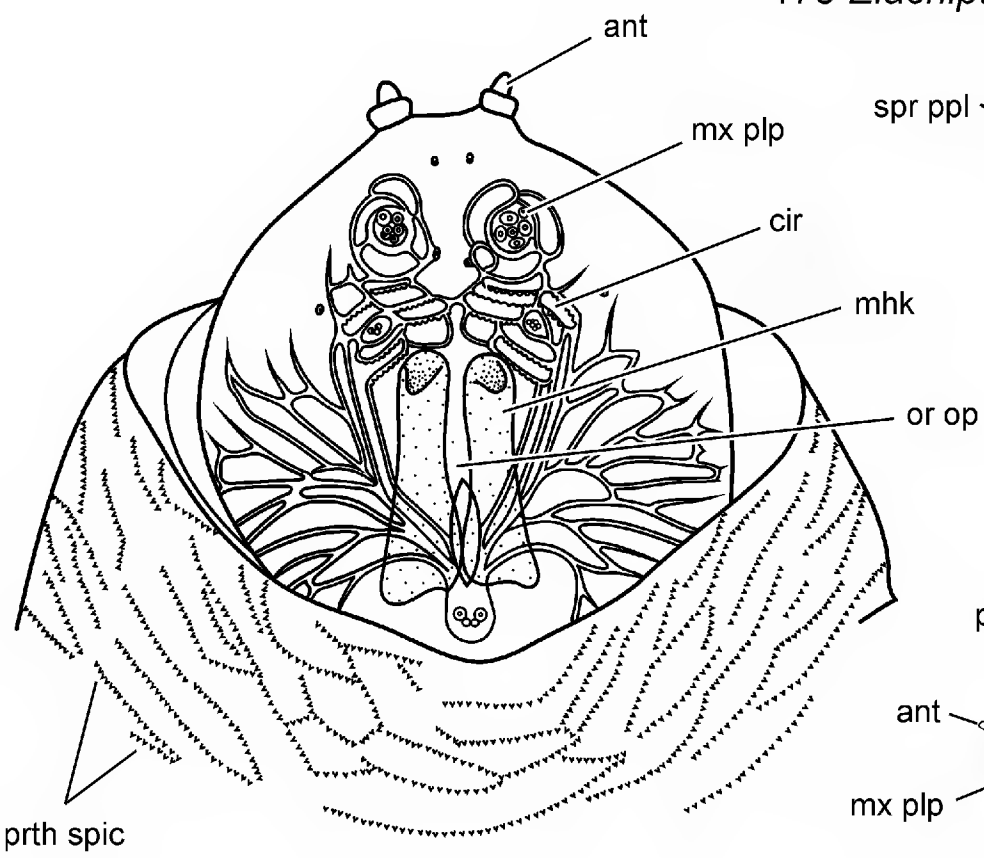
***Elachiptereicus* Becker** (Chloropinae)**.** A genus of nine valid species (Fig. 52), occurring in the Afrotropical, Australasian, Oriental and Palaearctic Regions (Evenhuis & Pape 2020; M. von Tschirnhaus, pers. comm. 2021). Three species are

recorded from the Afrotropics: *E. abessynicus* (Fig. 52), described from Ethiopia and recorded from East, Central, Southern, West Africa and the Southern Arabian Peninsula; *E. angustigena* Sabrosky, 1951, recorded from Nigeria and South Africa; and *E. bistriatus* Becker, 1909, recorded from Cameroon, Ethiopia, Lesotho, South Africa and Yemen (Deeming & Al-Dhafer 2012; Evenhuis & Pape 2020). Confirmatory characters include: arista thickened, flattened and blade-like (Fig. 52); ocellar triangle with line of setulae within lateral margins (at least in *E. abessynicus*); scutum with only prescutellar dorsocentral setae developed; anepisternum bare; wing crossveins *r–m* and *dm–m* closely approximated, separated by a distance less than length of *dm–m* (Fig. 52); hind femur less than twice as broad as tibia; and legs without organs on hind tibia and mid femur. The immature stages of *E. abessynicus* develop in the shoots of the grass *Rottboellia* and rarely of millets. Deeming (1977) provided detailed descriptions of the third-instar larva (including the cephaloskeleton) and the puparium of *E. abessynicus*. Sabrosky (1951: 721) provided an identification key to Afrotropical species.

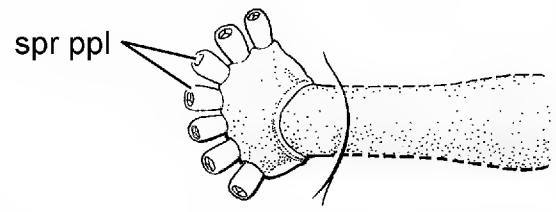
***Epimadiza* Becker** (Oscinellinae)**.** A genus of 24 valid species (Fig. 54), occurring in the Afrotropical, Oriental and Palaearctic Regions, with greatest diversity in the Afrotropics (Sabrosky 1947), where 24 species are recorded from all regions (Deeming & Al-Dhafer 2012; Evenhuis & Pape 2020). A number of additional undescribed species are known from Namibia and South Africa (J.W. Ismay, pers. obs.). Confirmatory characters



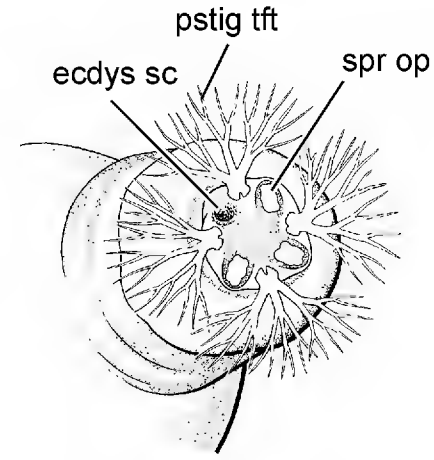
176 *Elachiptera*



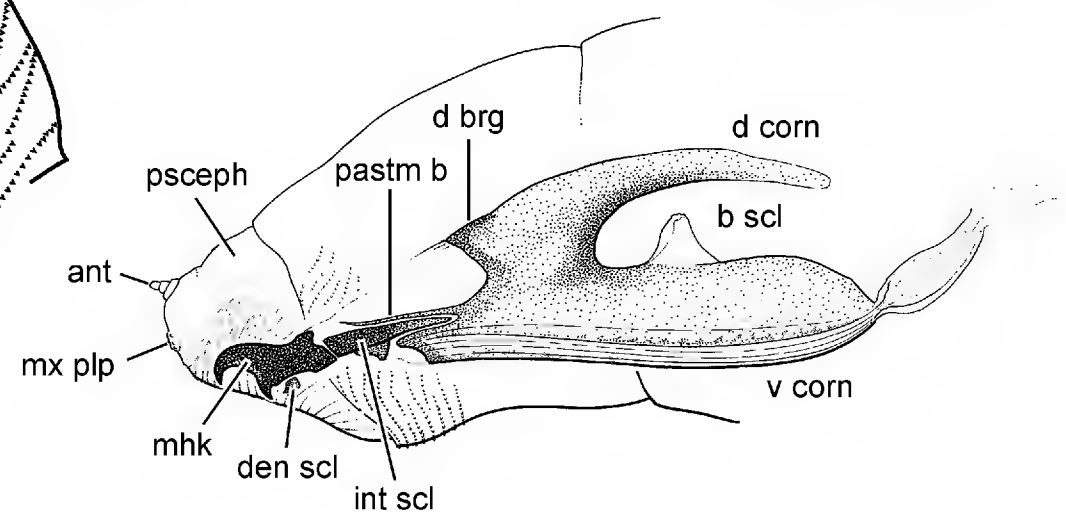
177 *Calamoncosis*



178 *Elachiptera*



179 *Elachiptera*



180 *Elachiptera*

Figs 96.176–180. Immature stages of Chloropidae (all non-Afrotropical): (176) larval habitus of *Elachiptera* sp., lateral view; (177) pseudocephalon and prothorax of larval *Calamoncosis glyceriae* Nartshuk, ventral view; (178) prothoracic spiracle of *Elachiptera* sp., lateral view; (179) same, posterior spiracle, caudal view; (180) same, larval pseudocephalon and cephaloskeleton, lateral view. Figs 176, 178–180 (Sabrosky 1987, figs 68, 69, 71, 70, respectively), Fig. 177 (Andersson 1977, fig. 17).

Abbreciations: ant – antenna; b scl – basal sclerite; cir – cirri; cr wlt – creeping welts; d brg – dorsal bridge; d corn – dorsal cornu; den scl – dental sclerite; ecdys sc – ecdysial scar; int scl – intermediate sclerite; mhk – mouthhook; mx plp – maxillary palpus; or op – oral opening; p spr – posterior spiracle; pastm b – parastomal bar; prth spic – prothoracic spicules; prth spr – prothoracic spiracle; psceph – pseudocephalon; pstig tft – peristigmatic tuft; spr op – spiracular opening; spr ppl – spiracular papillae; v corn – ventral cornu.

include: postpedicel rounded (Fig. 54); gena broad, characteristically divided diagonally from vibrissal angle dorsally to occiput, dorsal part dull (without setulae) and ventral part shiny; facial carina strong and distinct, although usually narrow; postocellar setae stout, straight and parallel; oral opening short and broad; proboscis short and inconspicuous; scutum densely and strongly punctured (but in many species not arranged in regular rows) (Fig. 54); anepisternum bare; notopleural setae 1 + 1; scutellar disc flattened; usually with 3–7 pairs of lateral scutellar setae; wing cell *br* strongly broadened in many species; fore femur enlarged (Fig. 157), with posteroventral ridge with row of spines or denticles in all species (very small in *E. nigrescens* (Dawah *et al*. 2020, fig. 19); lacking in *E. fascipennis*, an aberrant species distinguished by three black fasciae on wing; hind tibia without apical or subapical spur; and hind tibial organ present, but without mid femoral organ. In the Afrotropics, the immature stages of two species are known to be primary invaders of plants and can cause economic damage to cultivated plants, these being gladioli stems (the Gladioli fly, *E. hirta*) and seedlings of the Kapok tree (Ferrar 1987: 111). *Epimadiza gallicola* is thought to feed on decaying plant tissue (saprophagous) and has been found in galls on a shrub and on damaged cotton bolls (Ferrar 1987: 111). It has also been encountered in considerable numbers from fallen mahogany fruits damaged by a pyralid moth larva in Nigeria and from puparia in frass of the False codling moth in citrus in Nigeria (Deeming & Al-Dhafer 2012). *Epimadiza nigrescens* was reared from millet heads, Sorghum shoots and decaying lettuce in Nigeria, all of which may have been damaged by other insects (Dawah *et al*. 2020). Deeming & Al-Dhafer (2012) described the puparium of *E. gallicola* and illustrated the prothoracic spiracle and cephaloskeleton. Sabrosky (1947) provided an identification key to world species.

***Eribolus* Becker** (Oscinellinae)**.** A genus of eight valid species (M. von Tschirnhaus, pers. comm. 2021) (Fig. 55), occurring in the Nearctic and Palaearctic Regions. One undescribed species is known from South Africa in the Afrotropics. Confirmatory characters include: several irregularly enlarged frontoorbital setae present (Fig. 55); face with broad facial carina separating antennae; scutum flattened on disc (Fig. 55); and erect apical scutellar setae displaced to centre of scutellum. Larvae of extralimital species are known to be scavengers in plants that have been damaged by other insects (Valley *et al*. 1969), but the immature stages remain unknown. No identification key to species is currently available.

***Eutropha* Loew** (Chloropinae)**.** A genus of 23 valid species (Fig. 56), occurring in the Afrotropical, Australasian, Oriental and Palaearctic Regions (Deeming & Al-Dhafer 2012; Evenhuis & Pape 2020; M. von Tschirnhaus, pers. comm. 2021). Five species are recorded from the Afrotropics: *E. dancei* Deeming & Al-Dhafer, 2012 from Oman and Yemen; *E. lindneri* (Fig. 56) from South Africa; *E. longicornis* Deeming & Al-Dhafer, 2012 from Palaearctic Saudi Arabia and from Oman and Yemen; *E. obscura* Sabrosky, 1959 from Namibia and South Africa (Evenhuis & Pape 2020); and *E. siphloidea* (Duda, 1930) from Oman and United Arab Emirates. Confirmatory characters include: arista scarcely longer than remainder of antenna (except in *E. longicornis*, in which this longer and black) (Fig. 56); ocellar triangle moderately sized, not reaching anterior margin of frons; gena depth equal to 0.5 or more depth of eye (Fig. 56); more than 3–4 pairs of fronto-orbital setae developed, increasing in size from anterior to posterior; scutum pilosity pale; anepisternum bare; width of wing cell r_{2+3}, at apex of vein R_1 subequal to cell r_{4+5} (Fig. 56); hind tibia uniformly setulose, without discrete tibial organ; hind femur less than twice as broad as tibia; and male terminalia without band-shaped sclerites lateral to anus and surstylus free from epandrium. *Eutropha lindneri* (Fig. 56) was reared from decaying Cape fur seal carcasses on the Namibian coast (Kirk-Spriggs *et al*. 2001*a*) and the third-instar larva and puparium were described (Kirk-Spriggs 2007). The genus is almost invariably recorded from coastal habitats. Sabrosky (1972) provided an identification key to the then known species.

***Gampsocera* Schiner** (Oscinellinae)**.** A genus of 43 valid species (Fig. 57), occurring in the Australasian, Neotropical, Oriental and Palaearctic Regions (Evenhuis & Pape 2020; M. von Tschirnhaus, pers. comm. 2021). One undescribed Afrotropical species has been examined from Mauritius (J.W. Ismay, unpubl.). Confirmatory characters include: postpedicel longer than deep; arista flattened and sword-shaped, with long pubescence (Fig. 57); ocellar triangle smooth, without rows of punctures; facial carina absent; ocellar and postocellar setae convergent; pleura extensively shiny (in many species), at least anepisternum, anepimeron or katepisternum with extensive shiny area; notopleural setae 1 + 2; scutellum rounded, not longer than broad; lateral scutellar setae developed; hind tibia with tibial organ, but without apical or subapical spur; and without femoral organ on male mid femur. The species are sexually dimorphic, where males of some species have wing markings, but the female is unmarked, the epandrium is enlarged laterally into flanges, while the hypandrium has the phallic complex fused (Andersson 1977). The biology and immature stages remain unknown and there is no identification key available.

***Gaurax* Loew** (Oscinellinae)**.** A genus of 152 valid species (Fig. 58), occurring in all zoogeographical regions, except Antarctica (Tschirnhaus as cited in Kubík & Barták 2018). Four to five species are known from the Afrotropical Region distributed in East and Southern Africa, the Southern Arabian Peninsula, West Africa and the Indian Ocean Islands (Deeming & Al-Dhafer 2012; Evenhuis & Pape 2020). The four confirmed species are: *G. africanus* Sabrosky, 1951, described from Uganda; *G. amabilis* (Becker, 1913), recorded from Ethiopia, Kenya, South Africa and Yemen (Deeming & Al-Dhafer 2012; J.W. Ismay, unpubl.); *G. mycophagus*, described from Benin; *G. seychellensis* Lamb, 1912, described from Seychelles; and possibly *G. vittipennis* (Thomson, 1869), as it is recorded in Evenhuis & Pape (2020) as ?Rodrigues, following Sabrosky (1980). The genus was originally described from the Nearctic Region and it is doubtful that many species from other regions, currently ascribed to the genus, truly belong there and this requires considerable additional research. The Australasian and Oriental fauna is extensive, while relatively few species have been examined from the Afrotropics. Confirmatory characters include: postpedicel reniform, deeper than long; arista thin (Fig. 58); ocellar triangle smooth, without rows of punctures; facial carina absent; ocellar setae erect and cruciate; frontoorbital setae fine and evenly sized, none being markedly larger than remainder; postocellar setae erect, convergent or cruciate, shorter than outer vertical setae; pleura more extensively

shiny than pruinescent, at least anepisternum, anepimeron or katepisternum with extensive shiny areas (Fig. 58); anepisternum bare (Fig. 58); wing cell r_1 short and broad, opposite end of vein R_1 and much broader than cell r_{2+3}; vein R_{2+3} curved apically towards anterior of wing; costal cell (*c*) unusually broad, *ca* twice as wide as distal portion of cell *br*; second costal sector, less than 2.5 × as long as third sector (Fig. 145); scutellum not flattened dorsally, without finger-like projections or distinct tubercles; apical scutellar setae widely separated basally; hind tibial spur absent; and tibial organ present, but femoral organ on male mid femur absent. Some species in the genus (as currently defined), have been recorded from fungi and extralimital species from decaying plant material and insect egg masses (Ferrar 1987: 112). *Gaurax mycophagus* has been reared from fungi in central Benin (Nartshuk & Kurina 2014). Smith (1965) described the posterior spiracle and puparium of the Palaearctic *G. dubius* that had been reared from bracket fungi (Polyporaceae), while it is not clear if the other figures included in Ferrar (1987: 614–622) are of true *Gaurax* species, there is currently no published identification key to Afrotropical species.

***Hapleginella* Duda** (Oscinellinae)**.** A genus of five valid species (Fig. 59), occurring in the Afrotropical, Nearctic, Oriental and Palaearctic Regions (Deeming 2011; Evenhuis & Pape 2020). One described species has been recorded from the Afrotropics, *H. arabica* Deeming, 2011, is known from Oman, United Arab Emirates and Yemen (Deeming 2011: 790). Confirmatory characters include: body black and shiny (resembling *Oscinella*) (Fig. 59); postpedicel not reniform; arista slender (Fig. 8); ocellar triangle shiny, with several rows of small setulae within lateral margin (Fig. 8); facial carina barely developed; ocellar setae erect to slightly reclinate, usually convergent to cruciate; fronto-orbital setae fine and evenly sized, none much larger than remainder (Fig. 8); pleura extensively shiny, at least anepisternum, anepimeron or katepisternum with extensive shiny area; anepisternum bare; scutellum without finger-like projections or distinct tubercles; apical scutellar setae widely separated basally, with 1–2 pairs of lateral marginal setae; wing with first costal sector, shorter than second sector, less than 2.5 × as long as third sector; crossvein *r–m* located in basal half of wing; crossvein *dm–m* only slightly oblique or upright (Fig. 59); hind tibia without apical or subapical spur; mid femur with distinct femoral organ in male and hind tibia with tibial organ; and male terminalia with slender cerci and surstyli. The immature stages have been recorded in numerous papers dealing with insects in conifer cones in the Neotropical and Palaearctic Regions (some cited in Ferrar 1987: 113). Duda (1933: 78) identified specimens of *H. laevifrons* reared from cynipid galls, *Biorhiza pallida* (Olivier) (as *Andricus terminalis*) and Stadnitzky (1969: 148) reported dead insects as larval substrate. Conifer seeds repeatedly had been suspected, but have never been confirmed as food. The cephaloskeleton of the Palaearctic species *H. laevifrons* was described by Gaidene & Nartshuk (1963) and was figured in Ferrar (1987: 618) and Nartshuk (1987: 92, 97, 107) figured the larval pseudocephalon, the cephaloskeleton and the first and sixth thoracic segments of the larva. There is currently no identification key available.

***Heteroscinis* Lamb** (Oscinellinae)**.** An endemic genus of three valid species (M. von Tschirnhaus, pers. comm. 2021): *H. hystrix* (Séguy, 1957) (Fig. 60), recorded from Côte d'Ivoire, Nigeria and Sierra Leone; *H. ornata* Lamb, 1918, from Zimbabwe; and *H. variegata* Lamb, 1918, from Zimbabwe (Evenhuis & Pape 2020). Confirmatory characters include: postpedicel rounded apically; arista slender (Fig. 9); eye bare; face not carinate; frons shiny (Fig. 9); gena narrow, characteristically divided diagonally from vibrissal angle dorsally to occiput; ocellar setae erect to slightly reclinate (Fig. 9); postocellar setae stout, straight and parallel, slightly reclinate; scutum with fine punctures (arranged in rows in some species); anepisternum bare; notopleural setae 1 + 2; scutellum conical, narrow and elongate, much longer than wide and rounded at apex; scutellar marginal setae arising from lower margin (Fig. 60); hind tibia without apical or subapical spur; and hind tibial organ strongly developed. The biology and immature stages remain unknown. There is currently no identification key available.

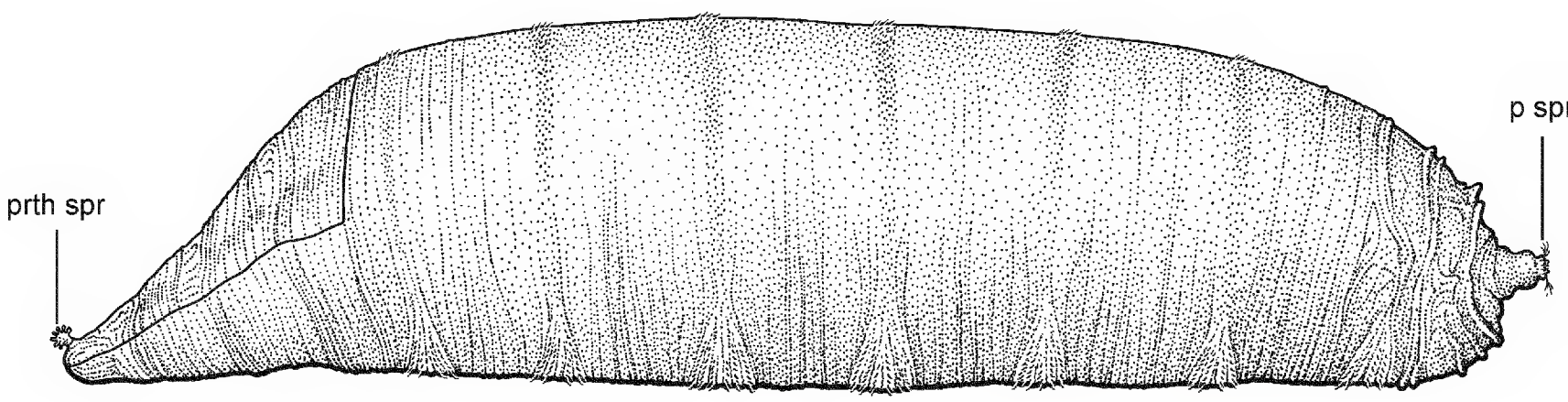
***Hippelates* Loew** (Oscinellinae)**.** A genus of 36 valid species (Fig. 61) occurring in the Afrotropical, Nearctic, Neotropical, Oriental and Palaearctic Regions (Deeming & Al-Dhafer 2012; Evenhuis & Pape 2020). The name *Hippelates* has been applied in the Old World for species with a strong anteroventral tibial spur, but these species have now been removed to other genera (*Arcuator* and *Cadrema*), that are not closely related to *Hippelates*. In the New World, species have been removed to several genera, including the closely related *Liohippelates*, a genus that is also of economic importance. One species of true *Hippelates* is known from the Afrotropical and Oriental Regions, but this almost certainly represents an introduction from the New World. *Hippelates proboscideus* Williston, 1896 (Fig. 61) was recorded from United Arab Emirates in 2005 (Deeming 2011: 792). Confirmatory characters include: postpedicel round (not reniform); arista slender (Fig. 61); ocellar triangle pruinescent with large shiny macula in apical section; ocellar setae erect and virtually parallel; facial carina blade-like and well-developed; scutum pruinescent, with three weakly developed long lines of punctures (Fig. 61); pleura extensively shiny in ventral half; anepisternum bare; scutellum much broader than long; wing with apical section of vein M_1 straight (Fig. 61); hind tibia with strong apical or anteroventral spur equal to, or longer than, diameter of tibia; and well-developed tibial organ present. In the United States, larvae have been found in damp soil or as leaf-miners and adults are eye-gnats (Ferrar 1987: 107), attracted to mammalian eyes, including humans and are implicated in the transmission of several diseases (Deeming 2011: 791). *Hippelates proboscideus* is known as a leaf-miner of Spider lilies, *Hymenocallis* sp. (Amaryllidaceae) and has been reared from tunnels in *Amaryllis* (Amaryllidaceae) bulbs, while an unknown *Hippelates* species was recorded as a leaf-miner of the Southern Swamp Lily, *Crinum americanum* L. (Amaryllidaceae), outside the Afrotropical Region (Nartshuk 2014; Stegmaier 1967), but the immature stages have not been described.

***Homops* Speiser** (Chloropinae)**.** A genus of 14 valid species (Fig. 62), occurring in the Afrotropical and Palaearctic Regions (Dawah *et al*. 2020; Evenhuis & Pape 2020; M. von Tschirnhaus, pers. comm. 2021). The 14 Afrotropical species are distributed in Central, East, Southern and West Africa and the Indian Ocean Islands (Deeming & Al-Dhafer 2012; Evenhuis & Pape 2020). Confirmatory characters include: body yellow to black in colour and nearly spherical in shape (Fig. 62); postpedicel shorter than deep; arista thin (Fig. 62); head unusually large and broader than thorax; eye large, occupying almost

entire head in profile; gena linear (Fig. 62); ocellar triangle rounded anteriorly, occupying most of frons, with at most a thin fascia (not broader than an ocellus), between margin of triangle and eye margin; head setae virtually all absent, except for minute vestiges of fronto-orbital setae; scutum smooth, shiny and highly convex, in lateral view extending as far above ventral margin of notopleuron as ventral margin of katepisternum ventrally (Fig. 62); scutal setulae greatly reduced or absent, scutum appearing entirely bare of setulae, with at most a single row present along dorsocentral line, very strongly arched, appearing hemispherical; scutellum flattened on disc with lateral margin angled; apical scutellar setae closely approximated; and hind tibia with distinct tibial organ present. The biology and immature stages remain unknown. Séguy (1933) provided a partial identification key to species, but see also Sabrosky (1951: 732), who incorporated additional species into this key.

***Kwarea* Sabrosky** (Oscinellinae)**.** A genus with two valid species, occurring in the Afrotropical and the Palaearctic Regions (Dawah *et al*. 2020; Evenhuis & Pape 2020). *Kwarea pallidihirta* Sabrosky, 1954 (Fig. 115) was described from Tanzania (Evenhuis & Pape 2020; Sabrosky 1954), while *K. ismayi* Deeming, 2020, was described from the Farasan Is. group in the Red Sea (Saudi Arabia) (Dawah *et al*. 2020), an island with a strong Afrotropical influence (J.C. Deeming, unpubl.). There is one additional undescribed species known from East and Southern Africa. Confirmatory characters include: postpedicel reniform; ocellar triangle not extending anteriorly beyond middle of frons and remainder of frons clothed in fine setulae (Fig. 10); facial carina undeveloped; ocellar setae proclinate and divergent; postocellar setae parallel; 2–3 longer fronto-orbital setae developed, equal to or longer than ocellar setae; remaining setae greatly reduced (Fig. 10); notopleural setae 1 + 1 well-removed from ventral margin of notopleuron; anepisternum bare; scutellum slightly broader than long and slightly rounded; scutal setulae short, dense and irregularly arranged; wing with second costal sector, *ca* twice as long as the third sector; cell *br* long and narrow, not wider at separation of veins R_{2+3} and R_{4+5} (Fig. 115); and femoral organ in *K. pallihirta* absent, but present in *K. ismayi* and with hind tibial organ. The biology and immature stages remain unknown.

***Lagaroceras* Becker** (Chloropinae)**.** A genus of 23 valid species (Figs 1, 63), occurring in the Afrotropical, Australasian, Oriental and Palaearctic Regions (Deeming 1981*a*, 2011; Deeming & Al-Dhafer 2012; Evenhuis & Pape 2020; M. von Tschirnhaus, pers. comm. 2021). Fifteen species are known from the Afrotropics, distributed in East, Southern and West Africa and the Southern Arabian Peninsula (Dawah *et al*. 2020; Deeming 1981*a*; Deeming & Al-Dhafer 2012; Evenhuis & Pape 2020). Confirmatory characters include: postpedicel at least 1.5 × as long as deep; arista white, densely pubescent, appearing slightly thickened (basal segments yellow in many species) (Fig. 63); ocellar triangle partly shiny, extending from mid length of



181 *Elachiptera*

182 *Steleocerellus*

Figs 96.181–182. Immature stages of Chloropidae: (181) puparial habitus of *Elachiptera* sp., lateral view (non-Afrotropical); (182) same, *Steleocerellus latiseta* (Lamb), ventral view (inset: ventral puparial cap). Fig. 181 (Sabrosky 1987, fig. 72).

Abbreviation: d pup cap – dorsal puparial cap; p spr – posterior spiracle; prth spr – prothoracic spiracle; v pup cap – ventral puparial cap.

frons to anterior margin (albeit in some species as linear extension); scutum in most species (but not *L. opaculum*) entirely black, not fasciate; anepisternum bare; wing crossveins *dm–m* and *r–m* separated by distance much greater than length of *dm–m* (Fig. 63); hind tibia uniformly setulose, without distinct tibial organ; male terminalia with surstylus usually extensively fused to epandrium; postgonites short; and pre- and postgonite in alignment. In Nigeria, *L. annulatum* and *L. pulchellum* and in Kenya, *L. princeps* (Becker, 1910), have been reared from a variety of grasses (Deeming 1981*a*). Deeming (1981*a*) described the puparia and cephaloskeletons of *L. annulatum* and *L. pulchellum* and figured the prothoracic puparial spiracles of *L. annulatum*, *L. pulchellum* and the Oriental species *L. tenuicorne*. Deeming (1981*a*) provided an identification key to most Afrotropical species, in which the recently described species *L. albolineatum* Deeming, 2011 and *L. argillum* Deeming & Al-Dhafer, 2012 key out as *L. curtum* Sabrosky, 1961. These two species can be identified by reference to Deeming (2011: 797) and Deeming & Al-Dhafer (2012).

***Lasiambia* Anonymous** (Oscinellinae)**.** A genus of 17 valid species (Fig. 64), occurring in the Afrotropical and Palaearctic Regions (Deeming & Al-Dhafer 2012; Evenhuis & Pape 2020; Nartshuk 1997). Five described species are recorded from the Afrotropics: *L. albidipennis* (Strobl, 1893) (Figs 11, 64), recorded from United Arab Emirates; *L. atritibia* (Sabrosky, 1951), described from South Africa; *L. brevibucca* (Duda, 1933), recorded from United Arab Emirates; *L. cephalotes* (Séguy, 1938), recorded from Kenya and Tanzania; and *L. rhodesiae* (Duda, 1936), from Zimbabwe (Deeming & Al-Dhafer 2012; Evenhuis & Pape 2020). Nicolai (1989) reported an undescribed species (as *Fiebrigella* spec. nov.) from the bark of trees in South Africa. At least ten undescribed species are known from East, Southern and West Africa and Dawah *et al*. (2020) recorded and figured an undescribed species from Saudi Ariabia, on the border with Yemen. Confirmatory characters (including some not apparent in non-Afrotropical species) include: postpedicel rounded apically (Figs 11, 12); eye bare, with long axis diagonal (Figs 11, 64); frons shiny (in some species dulled by microsculpture), with conspicuous piliferous punctures (often appearing as dark maculae); ocellar triangle (in some species), not sharply demarcated; gena broad, characteristically divided diagonally from vibrissal angle dorsally to occiput (with an angled ridge-like margin separating these areas), in many species ventral part smooth and shiny (often with distinct setulae), dorsal part dulled (without setulae) (Fig. 11); facial carina strong and distinct, although usually narrow (Fig. 12); ocellar setae erect to slightly reclinate, parallel to cruciate; postocellar setae stout, straight and parallel, slightly reclinate (Fig. 11); oral opening narrow, longer than broad; proboscis variable in length; scutum densely and strongly punctured (in many species punctures not in regular rows) and two faint grooves may be present along dorsocentral lines; anepisternum without setulae, but with pruinescence or fine pile (without sockets at base); notopleural setae 1 + 1; scutellum broad, with disc flattened (or virtually so); lateral scutellar setae not numerous, usually 3–7 pairs; wing crossvein *dm–m* at least slightly oblique; wing cell *br* strongly broadened in some species (including in *L. cephalotes*) (Fig. 64); femora not enlarged, without ventral spines; male femoral organ absent; and without anteroventral tibial spur or posterior tibial organ. The life histories of the genus are poorly understood and varied. Some species have been recorded as egg predators of Orthoptera, from rotting sweet potato and from stems of *Conium* in Europe (Ferrar 1987: 112, as *Fiebrigella*). In Germany, an undescribed species develops gregariously in the breeding cells of the bee *Megachile genalis* Morawitz (Megachilidae) nesting in living stems of the Glandular globe-thistle, *Echinops sphaerocephalus* (L.) (Asteraceae), where they consume pollen and cocooned dead *Megachile* larvae (M. von Tschirnhaus, pers. comm. 2021). Ferrar (1987: 613) illustrated the cephaloskeleton of *L. oophila*. Sabrosky (1951: 769) provided an identification key to three of the five described Afrotropical species (as *Goniopsita* Duda).

***Lasiochaeta* Corti** (Oscinellinae)**.** A genus of 35 valid species (Fig. 65), occurring in the Afrotropical, Oriental and Palaearctic Regions (Liu *et al*. 2017*b*; M. von Tschirnhaus, pers. comm. 2021; Tschirnhaus 2017). Fourteen species are recorded and are widely distributed in the Afrotropical Region (Tschirnhaus 2017). The genus was formerly referred to as *Melanochaeta* Bezzi, but the writers follow Nartshuk & Tschirnhaus (2012) in applying the name *Lasiochaeta* for this taxon. Confirmatory characters include: arista flattened and sword-shaped, with long pubescence; ocellar triangle smooth, without rows of punctures (Fig. 65); facial carina absent; ocellar setae short, erect and cruciate; postocellar setae erect and cruciate (in most species); two pairs of fronto-orbital setae enlarged (Fig. 65); scutum often with faint grooves along acrostichal and dorsocentral lines; pleura extensively shiny; anepisternum bare; scutellum short, broadly rounded apically, with disc convex; scutellar setae slender, not arising from distinct tubercles, 1–2 pairs of lateral scutellar setae developed (Fig. 135); male mid femur with femoral organ developed as single row of setae; and hind tibia with tibial organ, but without apical or subapical spur. The immature stages are known from the stems of grasses, but have not been described. *Lasiochaeta vulgaris* has been reared in 1993 and 1997 from cultivated Barley, Sorghum, Tef and Wheat in Ethiopia and from cultivated Wheat in Nigeria (J.C. Deeming, unpubl.). Deeming (1972: 13) recorded *L. scapularis* (Adams, 1905) having been reared from Maize and Sorghum in Nigeria. It was also reared in Nigeria from Finger millet shoots, *Eleusine coracana* that had been damaged by *Steleocerellus singularis* Becker, 1913 (J.C. Deeming, unpubl.). Finger millet is an important food crop in arid and semiarid parts of East Africa (Royal Botanical Gardens 2020). Sabrosky (1951: 784) provided an identification key to five Afrotropical species and Deeming & Al-Dhafer (2012) keyed five species occurring in the Arabian Peninsula, some of which are widespread in the Afrotropics.

***Lasiosina* Becker** (Chloropinae)**.** A genus of 54 valid species (Fig. 66), occurring in all zoogeographical regions, except the Neotropical Region and Antarctica (Deeming & Al-Dhafer 2012; Evenhuis & Pape 2020; M. von Tschirnhaus, pers. comm. 2021). Four species are known from the Afrotropics (Deeming & Al-Dhafer 2012; Evenhuis & Pape 2020), distributed in East, Southern and West Africa and the Southern Arabian Peninsula, but there are several additional undescribed species known from Southern Africa. Deeming & Al-Dhafer (2012) noted that the three longer fronto-orbital setae are much smaller in Afrotropical species than in Palaearctic species, including the type species. Confirmatory characters include: postpedicel at most 1.25 × as long as deep; arista black and thin (Figs 13, 66); fronto-orbital setae reduced to 3–4 slightly enlarged pairs (Figs 13, 66); wing with crossveins *dm–m* and *r–m* separated

by a distance much greater than length of *dm–m* (Fig. 66); hind tibia uniformly setulose, without discrete tibial organ; hind femur less than twice as broad as tibia; and male terminalia with surstylus (at least partially) fused to epandrium. Larvae of extralimital species are known to be secondary invaders of plant tissue (Ferrar 1987: 116) and Nartshuk & Andersson (2013: 196) recorded some Palaearctic species from grasses and cereals. Nartshuk & Andersson (2013: 233) figured the cephaloskeleton and the posterior end of the puparium of *L. herpini* (Guérin-Méneville, 1843). An identification key to all four Afrotropical species is not available, but Deeming & Al-Dhafer (2012), provided an identification key to the two species also occurring in the Arabian Peninsula, *L. apicata* (Becker, 1913) and *L. lucidifrons* (Becker, 1903).

***Leucochaeta* Becker** (Oscinellinae)**.** An endemic monotypic genus, with the single described species, *L. trapezina* Becker, 1913 (Figs 67, 116), recorded from Ethiopia and Rwanda (Evenhuis & Pape 2020). Confirmatory characters include: postpedicel *ca* 4 × as long as deep, flattened, with dorsal margin slightly concave in profile; arista white, with yellow base, appearing slightly thickened (due to flattened pubescence) (Figs 67, 116); eye bare; ocellar triangle shiny, without rows of punctures, but with frontal setulae on lateral margin; triangle extending broadly to anterior margin of projecting frons (Fig. 67); facial carina absent; ocellar and postocellar setae erect and convergent; fronto-orbital setae fine, evenly sized (Fig. 67); scutum without three lines of deeply incised punctures (Fig. 116); pleura extensively shiny; anepisternum bare (Fig. 116); notopleural setae 1 + 2; scutellum shorter than broad and trapezoidal; apical scutellar setae widely separated basally; and hind tibia without apical or subapical spur. The biology and immature stages remain unknown.

***Lipara* Meigen** (Oscinellinae)**.** A genus of eleven valid species (Fig. 117), occurring in the Australasian, Nearctic and Palaearctic Regions (Evenhuis & Pape 2020; Kanmyia 1982; Sabrosky 1980*b*; M. von Tschirnhaus, pers. comm. 2021). The genus is best known from the Palaearctic Region and probably represents an introduction in the Nearctic. The genus is not formally recorded from the Afrotropics, but an undescribed species is known from rainforest canopy fogging in Uganda (J.W. & B. Ismay, unpubl.). Confirmatory characters include: moderate to large species, densely clothed in setulae, with broad, dumpy appearance (Fig. 117); antennae small; postpedicel short and rounded (Fig. 14); antennal foveae concave (Fig. 14); eye pubescent (in many species) and long axis vertical (in most); head and scutum with setae reduced in size, but setulae long, very numerous and dense (making distinction between setae and setulae difficult) (Fig. 14); facial carina very strongly developed, broad and flat on anterior margin (Fig. 14); ocellar setae almost indistinguishable from head setulae; postocellar setae convergent, slightly longer than head setulae; anepisternum bare; male femoral organ developed into raised prominence, with numerous small setulae; hind tibia without apical or subapical spur; and hind tibial organ present. Larvae cause galls in the stems of Common reed and these are either used as biocontrol in areas where reed is regarded as a pest or they are termed "damaging" where reed is grown commercially. Grochowska (2011) provided a comprehensive account of the genus. Nartshuk & Andersson (2013: 1182) summarised the biology of the western Palaearctic species, including the sound communication of adults. Grochowska (2013) provided detailed descriptions of all immature stages of the non-Afrotropical species *L. lucens*. There is no identification key to all *Lipara* species, but Nartshuk & Andersson (2013: 118) provided keys to adults and larvae of the western Palaearctic species and Kanmyia (1983) provided a key to the five Japanese species. Over 350 publications and dissertations dealing only with the biology and ecology of *Lipara* species have been published (M. von Tschirnhaus, pers. comm. 2021).

***Meijerella* Sabrosky** (Oscinellinae)**.** A genus of five valid species (Fig. 68), occurring in the Afrotropical, Australasian, Oriental and Palaearctic Regions (Dawah *et al*. 2020; Deeming 2011; Evenhuis & Pape 2020). Two small, grey pruinescent species are known from the Afrotropics: *M. flavisetosa* Sabrosky, 1976, recorded from Yemen (Deeming 2011: 793) and *M. inaequalis* (Becker, 1911), described from Mauritius (J.W. Ismay, unpubl.). Confirmatory characters include: ocellar triangle and scutum heavily grey pruinescent; ocellar triangle with double row of setulae within margin, almost parallel to fronto-orbital setae; facial carina only developed between bases of antennae; ocellar and fronto-orbital setae very small and erect; scutum with three shallowly incised lines of punctures; pleura entirely pruinescent on (at least) anepisternum, anepimeron and katepisternum (Fig. 68); anepisternum bare; notopleural setae 1 + 1; postpronotal, dorsocentral and anterior notopleural setae very short; scutellum trapezoidal, with apical setae borne on small tubercles (posterior margin of scutellum appears concave) (Fig. 136); and large hind tibial organ present. The immature stages of extralimital species are known from rotting stems of rice and *Amaranthus* (Amaranthaceae) (Ferrar 1987: 113) and fruit of *Touchardia* (Urticaceae) (Deeming 2011: 793), but have not been described. Sabrosky (1976) provided an identification key to world species, including one undescribed species, but excluded *M. indica* Cherian, 1977.

***Melanum* Becker** (Chloropinae)**.** A genus of 10 valid species (Fig. 69), occurring in the Australasian and Palaearctic Regions (Evenhuis & Pape 2020; M. von Tschirnhaus, pers. comm. 2021). The genus is not formally recorded from the Afrotropics, but undescribed species are known from Ethiopia and Sierra Leone. The genus differs from *Chlorops* in the strongly acute to right-angled, anteriorly extended vibrissal angle (Fig. 69), the postpedicel is as long as deep or slightly shorter (Fig. 15) and in the male terminalia. Confirmatory characters include: ocellar triangle shiny, extending almost to anterior margin of frons; scutum black and slightly pruinescent; and hind tibial organ absent. The immature stages remain unknown, but Tschirnhaus (1981) reared it from *Juncus gerardii* Loisel (Juncaceae) in Germany. There is no recent identification key.

***Mepachymerus* Speiser** (Chloropinae)**.** A genus of 18 valid species (Fig. 70), occurring in the Afrotropical, Australasian, Oriental and Palaearctic Regions (Evenhuis & Pape 2020; M. von Tschirnhaus, pers. comm. 2021). *Mepachymerus* is represented by six Afrotropical species, distributed in East, Central, West and Southern Africa (Evenhuis & Pape 2020), where they are a conspicuous element of the grassland fauna. Confirmatory characters include: body, legs and wings more or less narrowly elongate (Fig. 70); arista thickened, flattened and blade-like; head longer than deep (Fig. 70); only two fronto-orbital setae developed; ocellar and postocellar setae minute; scutum almost entirely pruinescent; pleura mostly pruinescent;

anepisternum bare; thoracic setation greatly reduced (Fig. 70); postpronotal seta absent; 1 (posterior) notopleural seta developed (in most species); single posterior dorsocentral seta greatly reduced; wing crossveins *dm–m* and *r–m* not closely approximated, with cell *dm–m* elongate; anal lobe undeveloped (Fig. 70); legs very long and slender, with laterally compressed fore tarsus (Fig. 70); hind tibial organ absent; and male terminalia with pre- and postgonites narrow and discrete. Kirk-Spriggs (1986) provided detailed descriptions of the puparia, including the cephaloskeleton of two West African species. Sabrosky (1951: 724) provided an identification key for some species.

***Merochlorops* Howlett** (Chloropinae)**.** A genus of 26 valid species (Figs 71, 118), occurring in the Afrotropical, Australasian, Oriental and Palaearctic Regions (Evenhuis & Pape 2020; M. von Tschirnhaus, pers. comm. 2021). Three species are recorded from the Afrotropics: *M. ceylanicus* (Duda, 1930) (Figs 71, 118), recorded from United Arab Emirates (Deeming 2011: 799); *M. lucens* (de Meijere, 1908), from Mauritius, Réunion Is., Rodrigues Is. and Seychelles (Evenhuis & Pape 2020); and *M. vanharteni* Deeming & Al-Dhafer, 2012 (Fig. 16), described from Yemen in the Afrotropics and Palaearctic Saudi Arabia (Deeming & Al-Dhafer 2012). Confirmatory characters include: head unusually large, broader than thorax (Figs 71, 118); eye large, occupying almost entire head (viewed in profile) (Fig. 71); ocellar triangle narrow and pointed, ending at anterior margin of frons (Fig. 16); gena linear; scutum smooth, shiny and highly convex, but not hemispherical (in lateral view extending as far above ventral margin of notopleuron as ventral margin of katepisternum below) (Figs 71, 118); scutum mostly bare, except for a few setulae along dorsocentral lines and on an area broadening out from beyond suture to posterior margin; and hind tibia with distinct tibial organ. *Merochlorops flavipes* larvae have been reared from Ginger and *M. cardami* larvae from a Cardamom stem in India (Cherian 1991) and the puparium of *M. lucens* was described in the same paper. *Merochlorops flavipes* larvae are known to bore the stems of Cardamom and Ginger (Nartshuk *et al.* 2015). The Indian species *M. dimorphus* was investigated as a biocontrol agent of the invasive Ginger lily, *Hedychium gardnerianum* in India and in laboratory conditions in the United Kingdom (Djeddour *et al.* 2012) and this report includes images of a larva, puparium and adult. Nartshuk *et al.* (2015) provided an identification key to South-east Asian species, which includes two of the three Afrotropical species.

***Meromyza* Meigen** (Chloropinae)**.** A large genus of 101 valid species (Fig. 72), occurring in the Afrotropical, Nearctic, Neotropical, Oriental and Palaearctic Regions (Evenhuis & Pape 2020; M. von Tschirnhaus, pers. comm. 2021; Nartshuk 2012; Sabrosky & Paganelli 1984: 38). Only two species are recorded from the Afrotropics: *M. reclinans* Becker, 1914, recorded from Democratic Republic of Congo and Tanzania; and *M. incompleta* (Loew, 1860), restricted to South Africa (Evenhuis & Pape 2020). An undescribed species has been examined from Nigeria. An entirely black undescribed species was collected in Madagascar (M. Tschirnhaus, pers. comm. 2021) and this was examined by the senior author. Confirmatory characters include: postpedicel slightly longer than deep; arista slender, with short or minute pubescence; frons with anterior margin extending less than 0.5 × length of eye; ocellar triangle without setulae within lateral margin; parafacial broadened (visible in lateral view) (Fig. 72); outer vertical setae large; inner vertical setae small, but distinctly developed; pleura shiny (in part); anepisternum bare (in Afrotropical species); hind femur thickened, more than twice as broad as tibia, thicker than (at least) one other femur, with double row of minute, blunt, black ventral setae (Fig. 72); tibia correspondingly curved; and male terminalia with postgonites enlarged and projecting ventrally (unique feature). The form of the postgonites offers many specific characters, while the surstyli and phallus also have good features to distinguish species (Nartshuk & Andersson 2013: 201). The green larvae of extralimital species are recorded as primary invaders of stems of grasses and cereals and can cause economic damage (Ferrar 1987: 116). Balachowsky & Mesnil (1935: 959) illustrated the larvae of three Palaearctic species and Fedoseeva (1966) illustrated and described further larvae of Palaearctic species and provided an identification key. There is currently no identification key to Afrotropical species and there is no published figure of the male terminalia of *M. reclinans*.

***Meromyzella* Andersson** (Chloropinae)**.** An endemic monotypic genus, with the single valid species, *M. capensis* (Loew, 1866) (Fig. 119), widespread in East, Central, Southern and West Africa (Evenhuis & Pape 2020), occurring mainly in grassland habitats. Confirmatory characters include: body large, heavily pruinescent (Fig. 119); postpedicel *ca* as long as deep; arista black and slender, with short (or minute) pubescence (Fig. 119); ocellar triangle pruinescent, with single row of small setulae within lateral margins, extending almost to anterior margin of frons (Fig. 119); gena almost as deep as antennal postpedicel; parafacial narrow (not visible in lateral view); head setae short; one slightly enlarged vertical seta present; ocellar and postocellar setae slightly larger than setulae on frons, directed slightly anteriorly; wing veins R_{2+3} and R_{4+5} curved anteriorly and veins R_{4+5} and M_1 divergent (Fig. 119); hind femur thickened, more than twice as broad as tibia (thicker than at least one other femur); tibia correspondingly curved, without strong anteroventral row of thorn-like spines, but with double row of minute, blunt, black ventral setae (Fig. 158); and male terminalia without enlarged and projecting postgonites. Deeming (2018) recorded *Meromyzella* as being ovoviviparous, otherwise the biology and immature stages remain unknown.

***Metopostigma* Becker** (Chloropinae)**.** A genus of eight valid species (Fig. 73), occurring in the Afrotropical, Oriental and Palaearctic Regions (Evenhuis & Pape 2020; M. von Tschirnhaus, pers. comm. 2021). Two species are recorded from the Afrotropics: *M. sabulona* Becker, 1910, from Oman, United Arab Emirates and Yemen, in the Southern Arabian Peninsula (Deeming 2011: 799); and *M. tenuiseta* (Loew, 1860) (Fig. 73) is widespread in East, Southern and West Africa (Deeming & Al-Dhafer 2012; Evenhuis & Pape 2020). Confirmatory characters include: body pale, heavily pruinescent (Fig. 73); yellow with three broad, dull, reddish grey to black fasciae on scutum and two broad fasciae on abdomen on dorsal and ventral surfaces of tergites (may appear darkened); setae and setulae white (Fig. 73); postpedicel 1.3–1.5 × longer than deep; arista not thickened and flattened, but with white pubescence (Fig. 73); ocellar triangle yellow, pruinescent, with large, round, black and shiny macula anterior to ocelli; gena broad, broader than depth of postpedicel (Fig. 73); pleura pruinescent; anepisternum bare; scutellum large and flat, with apical scutellar setae not closely approximated; wing crossveins *dm–m* and

r–m not closely approximated, but separated by distance much greater than length of crossvein *dm–m* (Fig. 73); hind femur less than twice as broad as tibia; and narrow hind tibial organ present. The biology and immature stages remain unknown, but they have been collected by sweeping grasses and around Wheat seedlings in Saudi Arabia (Deeming & Al-Dhafer 2012). Afrotropical species were included in the identification key provided by Deeming & Al-Dhafer (2012).

***Microcercis* Beschovski** (Oscinellinae)**.** A genus of 28 valid species (Fig. 74) (including species formerly placed in *Incertella*), occurring in all zoogeographical regions, except the Australasian Region and Antarctica (Deeming & Al-Dhafer 2012; Evenhuis & Pape 2020; M. von Tschirnhaus, pers. comm. 2021; Nartshuk & Przhiboro 2009). There is currently confusion over generic limits with *Incertella* and it is not possible to accurately determine how many species should be included in both; these and two other genera require additional study to clarify the generic placements (Nartshuk & Przhiboro 2009). Deeming & Al-Dhafer (2012) and Tschirnhaus (2007) are here followed in treating *Incertella* as included in *Microcercis*. Two species are currently recorded from the Afrotropics: *M. albipalpis* (Meigen, 1830), from Oman; and *M. dimorphica* (Fig. 74) from Oman and Yemen (Deeming & Al-Dhafer 2012). Confirmatory characters include: arista not thickened; ocellar triangle pruinescent, without rows of small setulae within lateral margin; fronto-orbital setae fine and evenly sized, none much larger than remainder; postocellar setae erect and cruciate; scutum with setulae arranged in long rows (in *M. albipalpis*) or irregularly arranged (in *M. dimorphica*), without deeply incised lines of punctures; pleura partly shiny and pruinescent (Fig. 74); notopleural setae varying from 1 + 1 to 1 + 2 (in *M. albipalpis*) (Tschirnhaus 2007) or 1 + 2 (in *M. dimorphica*); wing vein M_1 not curved (in *M. dimorphica* with dark band at costal margin, from end of vein R_1 to beyond vein R_{2+3} (Fig. 74); hind tibial organ absent in *M. dimorphica*, but present in *M. albipalpis*; male mid femoral organ with two rows of setae in *M. albipalpis*, but these absent in *M. dimorphica*; hind tibia without apical or subapical spur; and male terminalia in *M. albipalpis* with hypandrium closed, but open in *M. dimorphica*. In *M. dimorphica*, there is considerable sexual dimorphism, in that the male has the frons strongly inflated and bearing numerous setulae, which is neither the case in the female nor in either sex in other species of the genus. The immature stages of extralimital species (as *Incertella*) are known from the stems of grasses and cereal crops (Nartshuk & Andersson 2013: 109) and Grochowska (2008*a*) provided detailed descriptions of all immature stages of the non-Afrotropical species *M. zuercheri* (as *Incertella*). Deeming & Al-Dhafer (2012) provided an identification key to the two described Afrotropical species.

***Mimosepsis* Sabrosky** (Oscinellinae)**.** An endemic genus of three valid species (Fig. 75): *M. mallochi*, *S. myrmecophila* Deeming, 1976 and *M. scutellaris*, all described from Nigeria (Evenhuis & Pape 2020). Confirmatory characters include: general habitus *Sepsis*-like (Sepsidae) (Fig. 75); head 1.2 × as long as high; eye with long axis nearly horizontal (Fig. 75); lower occiput with pair of long and straight setae, situated midway between neck and oral margin; ocellar setae erect, subparallel or slightly convergent; proboscis geniculate (Fig. 75); anepisternum with small setulae; abdomen strongly to slightly petiolate, with second segment also strongly constricted basally (except in *M. scutellaris*); hind tibial organ and male mid femoral organ undeveloped; male abdomen with only four visible segments, two greatly enlarged (except in *M. scutellaris*), while female abdomen with five apparent segments (Fig. 75); and female ovipositor as long as preabdomen (tergites 1–5). Adults have been found to occur in association with ants and have been recorded from a humid forest area in southern Nigeria (J.C. Deeming, unpubl.). The biology and the immature stages otherwise remain unknown. An identification key was provided by Deeming (1976).

***Neoloxotaenia* Sabrosky** (Chloropinae)**.** A genus of five valid species (Fig. 77), occurring in the Afrotropical, Australasian, Oriental and Palaearctic Regions (Deeming 2011: 802; Evenhuis & Pape 2020). One species, *N. gracilis* (Fig. 77), is recorded from Yemen in the Southern Arabian Peninsula (Deeming 2011: 802). Confirmatory characters include: antennal segments greatly elongated; arista thin and bare (Fig. 77); head setation greatly reduced; eye very large, occupying most of head (in lateral view), long axis vertical; ocellar triangle very large, reaching broadly to anterior eye margin, with minute setulae within lateral margins; gena linear; anepisternum bare; without discernible notopleural setae; wing crossveins *dm–m* and *r–m* separated by distance much greater than length of *dm–m*; cell *bm+dm* narrow (Fig. 77); femora less than twice as broad as tibiae; and hind tibial organ absent. *Neoloxotaenia gracilis* is a black species that has a silver diagonal fascia on the pleura. Larvae of *N. gracilis* have been found to develop in Cardamom in India (Deeming 2011: 802) and it was reared out of gregarious puparia from a shoot of the Ginger lily, *Hedychium gardnerianum* in Sikkim, India (Djeddour *et al*. 2012). Biology and immature stages otherwise remain unknown. An identification key to species was provided by Liu & Yang (2012).

***Nomba* Walker** (Oscinellinae)**.** A genus of seven valid species (Figs 78, 120), occurring in the Afrotropical, Australasian and Oriental Regions (Evenhuis & Pape 2020). Three described species are recorded from the Afrotropics: *N. beckeri* (Enderlein, 1920), from Equatorial Guinea and possibly Uganda; *N. chrysomelina* (Enderlein, 1920), from Equatorial Guinea and Sierra Leone and *N. saegeri* (Vanschuytbroeck, 1959), from Democratic Republic of Congo (Evenhuis & Pape 2020; Sabrosky 1980*b*: 701). Confirmatory characters include: genal setae enlarged and thickened (in some species); ocellar setae proclinate and divergent; postocellar setae long and cruciate; *ca* six fronto-orbital setae developed; scutum and scutellum rugose, surface roughly pitted, with dense setulae (Figs 78, 120); anepisternum setulose; scutellum very large, covering entire abdomen, rounded and rugose, broader at middle than at base, with numerous (more than six) pairs of setae inserted at regular intervals, often on small tubercles (Figs 78, 120); male mid femoral organ absent; fore femur with setae on ventral surface enlarged (in some species), or setae on ventral surface of hind femur enlarged and thickened in two rows, with enlarged bases; hind femur thickened in some species; and hind tibial organ absent. Extralimital species have been swept from tree trunks in rainforests (B. & J.W. Ismay, pers. obs.), the biology and immature stages otherwise remain unknown and no identification key to species is currently available.

***Notaulacella* Enderlein** (Oscinellinae)**.** A genus of 25 valid species (Fig. 79), originally described from the Neotropical Region (Evenhuis & Pape 2020; M. von Tschirnhaus, pers. comm.

2021) and now also known from the Nearctic Region (Barrie & Wheeler 2016), Afrotropical, Australasian and Oriental Regions (J.C. Deeming & J.W. Ismay, unpubl.), with at least seven undescribed species known from Nigeria alone. The genus is regarded as being placed within the subfamily Oscinellinae, following Wheeler (2010: 1138) and further comments are included under "Classification" above. Confirmatory characters include: body colour variable, from yellow to black (Fig. 79); ocellar triangle well-developed, shiny or pruinescent (Fig. 79); facial carina absent; gena narrower than fore tibia, with longer seta at anterior and posterior corners and *ca* five slightly enlarged setae between these; *ca* 4–5 longer, slightly reclinate fronto-orbital setae developed; ocellar setae proclinate and divergent (Fig. 79); postocellar setae cruciate; scutum with sparse, irregularly arranged setulae and large dorsocentral seta; anepisternum bare; notopleural setae 1 + 1; scutellum slightly broader than long and rounded, disc with sparse setulae; apical scutellar setae large, not borne on tubercles and smaller lateral pair developed; wing with second costal sector, more than twice as long as third sector; vein M_1 concave posteriorly, curving first towards R_{4+5}, then away from it; cell *bm+dm* very narrow; mid femoral organ developed in some species (Fig. 79); and hind tibial organ present. Biology and immature stages remain unknown and no identification key to Afrotropical species is currently available.

***Oscinella* Becker** (Oscinellinae)**.** A genus of 67 valid species (Fig. 80), occurring in all zoogeographical regions, except Antarctica (Deeming 2003; Evenhuis & Pape 2020; M. von Tschirnhaus, pers. comm. 2021). Thirty species are recorded from the Afrotropics, distributed in the Atlantic Ocean Islands, Central, East, Southern and West Africa, the Southern Arabian Peninsula and the Indian Ocean Islands (Dawah & Abdullah 2006; Deeming 2003, 2011: 793; Deeming & Al-Dhafer 2012; Evenhuis & Pape 2020), but the genus has been used in the past as a "dumping-ground" for a host of diverse species lacking the diagnostic characters needed to assign them to other genera (Deeming 2003). The genus *Oscinella* includes several subgenera of which *O.* (*Cyclocercula*) (two European species only), *O.* (*Paroscinella*) (three species only) and *Oscinella sensu stricto* occur, although many species of *Oscinella* have not been assigned to a subgenus. Confirmatory characters include: postpedicel *ca* as long as deep; arista slender, with short microtrichia or bare (Fig. 80); eye short-pubescent or bare; ocellar triangle bare and shiny and varying in length from two-thirds length of frons to anterior margin of frons (Fig. 80); anterior margin of frons varying from concave to moderately convex; facial carina absent; orbital setae fine, evenly sized, none much larger than remainder; ocellar setae erect and cruciate, inserted within ocellar tubercle; postocellar setae erect, usually convergent or cruciate; scutum with setulae arranged in regular, long lines, their separation greater than length of setula (Fig. 80); pleura with dorsal part either shiny, or with small patch of pruinescence anterior to mid coxa; anepisternum bare; notopleural setae 1 + 2; scutellum shorter than wide, usually broadly rounded in outline; apical scutellar setae not on tubercles and usually widely separated basally, with 1–2 pairs of lateral setae; wing cells r_1 and r_{2+3} subequal in width; crossvein *r–m* situated in basal half of wing, crossvein *dm–m* only slightly oblique or right-angled to vein R_{4+5} (Fig. 147); hind tibial organ present, but tibial spur absent; and male mid femoral organ expressed as single row of setae. Larvae of some species are known to invade the stems of grasses, causing the meristem (the growing point of the shoot) to die and leading to economic damage to cereal and fodder crops, including millets, rice and Sorghum. Ferrar (1987: 113) provided a short summary of the biology of the genus, including an overview of larval hosts and feeding mechanisms and further references. Nartshuk & Andersson (2013: 124) included detailed information on the biology of some Palaearctic species and of *O. nitidissima* and also commented on the *O.* (*O.*) *frit* complex. Deeming (2003) provided an identification key to Afrotropical species of the subgenus *O.* (*Paroscinella*) and included a detailed description of the third-instar larva and puparium of *O.* (*C.*) *nartshukiana*, including several figures of both and a detailed description of the puparium, including figures of the cephaloskeleton and prothoracic spiracle of *O. nitidigenis*. Balachowsky & Mesnil (1935: 1000–1003, 1015–1016, 1019) provided figures and descriptions of larvae and puparia of three Palaearctic species, including *O.* (*O.*) *frit*. Ferrar (1987: 613) included figures of all immature stages, except the first-instar larvae and the cephaloskeleton of *O.* (*O.*) *frit* and the third-instar larva and cephaloskeleton of the Palaearctic species *O. vastator*. Nartshuk (1987: 87) gave detailed figures of immature stages of several species of *Oscinella*, including the third-instar larva and cephaloskeleton of the Afrotropical species *O. nitidissima*. Nartshuk & Andersson (2013: 134) illustrated the spicules on the ventral surface of the larva of *O. nitidissima*. There are some species of *Conioscinella* with a shiny triangle and these might key out here, but they do not have setulae on the scutum arranged in long lines and differ in other characters.

***Oscinimorpha* Lioy** (Oscinellinae)**.** A genus of 13 valid species (Fig. 81), occurring in the Afrotropical and Palaearctic Regions (Evenhuis & Pape 2020; M. von Tschirnhaus, pers. comm. 2021). Four undescribed species are known from Namibia and South Africa (Ismay 2000). Confirmatory characters include: body colour variable from yellow to black, antennae small, with postpedicel short and rounded (Fig. 81); head higher than long; eye short setulose; ocellar triangle pruinescent, without setulae within lateral margins, ending well before anterior margin of frons; facial carina weakly developed; vibrissal angle acute (Fig. 81); ocellar setae erect and convergent; postocellar setae erect and slightly convergent; palpus narrow and elongate (equal to, or longer than, oral cavity); proboscis elongate (much longer than oral cavity) and heavily sclerotised (Fig. 81); scutum with setulae irregularly arranged; anepisternum bare and pruinescent ventrally; wing with second costal sector, longer than third sector (Fig. 81); hind tibial organ present, but tibial spur absent; and male mid femoral organ consisting of single row of setae. This genus occurs in grasslands and sandy habitats in the Palaearctic and the European species *O. albisetosa* (Duda, 1932) has been reared from the grasses *Elytrigia* and *Puccinella* (Poaceae) and it may be phytophagous (Nartshuk & Andersson 2013: 135), the European species *O. minutissima* (Strobl, 1900), has been reared from Clary sage, *Salvia sclarea* L. (Lamiaceae), the grass *Secale* (Poaceae), the rice *Oryza* (Poaceae) and Red campion, *Silene dioica* (L.) Clairv. (Caryophyllaceae) (Nartshuk & Andersson 2013: 135; Tschirnhaus 1981: 75), although Nartshuk (2014) regarded it as saprophagous. The immature stages remain unknown and there is no identification key to Afrotropical species.

***Pachylophus* Loew** (Chloropinae)**.** A genus of 34 valid species (Fig. 82), occurring in the Afrotropical, Australasian, Oriental and Palaearctic Regions (Deeming 2018). The Afrotropics

is the most diverse region, with 26 valid species (Deeming 2018), distributed in Central, East, Southern and West Africa, the Southern Arabian Peninsula and the Indian Ocean Islands, principally in grassland habitats. Confirmatory characters include: pedicel with ventral projection (varying in development between species); postpedicel more or less reniform; arista broadened or at least with long dense microtrichia, appearing broad and flat (Fig. 82); frons length variable, either not projecting beyond anterior margin of eye or may be greatly produced; ocellar triangle with single row of setae within lateral margins, reaching almost to anterior margin of frons; face receding; facial carina poorly developed; gena *ca* as broad as depth of postpedicel (Fig. 82); inner and outer vertical setae both developed; fronto-orbital setae small, with *ca* eight setae developed; postpronotum with only small setulae; anepisternum bare (except in *P. pellucidus* Becker, 1910, where setulose in posterior half and *P. ismayi* Deeming, 2018, which has upper margin with several rows of minute, compact erect setulae); notopleural setae small 1 + 1; hind femur thickened, but degree of thickening varying between species from more than twice as broad as tibia (in most species) to thicker than at least one other femur (Fig. 82); and tibia correspondingly curved. The genus is ovoviviparous and larvae have been found in the stems of grasses and cereals including rice, but in many cases are thought to be secondary invaders after damage by other insects (Deeming 2018). Deeming (1974) described the third-instar larva and the puparium of *P. beckeri*; Deeming (1977) described the third-instar larvae and the puparium of *P. lugens*. Spencer (1985: 79) figured the cephaloskeleton of *P. punctifemur*. *Pachylophus beckeri* is a major pest of rice in West Africa (Deeming 2018). Deeming (2018) provided an identification key to Afrotropical species, which included the description of the puparia of several species.

***Parectecephala* Becker** (Chloropinae)**.** A genus of 32 valid species (Fig. 83), occurring in all zoogeographical regions, except Antarctica (Evenhuis & Pape 2020; M. von Tschirnhaus, pers. comm. 2021). There are five Afrotropical species, recorded from Kenya, Namibia, Nigeria, Tanzania, Yemen, Zambia and Zimbabwe (Deeming & Al-Dhafer 2012; Evenhuis & Pape 2020). Confirmatory characters include: antennal postpedicel distinctly longer than deep, at least 1.5 × as long as deep; arista with basal segments yellow, remainder white, densely pubescent, appearing slightly thickened (Fig. 83); ocellar triangle large, shiny and bare, almost reaching anterior margin of frons (Fig. 83); ocellar, postocellar and inner and outer vertical setae small; proboscis short; scutum yellow, with black fasciae and an anterior, rounded, velvety black macula on inner lateral fascia (Fig. 83); one postpronotal seta; notopleural setae 1 + 2; hind femur less than twice as broad as tibia; hind tibia without tibial organ; male terminalia with postgonites long, more or less fused with phallapodeme, parallel to pregonites (as in *Chlorops*); and surstylus discrete from epandrium. *Parectecephala gigas* has been reared in Uganda from shoots of grasses (*Pennisetum* spp.) and the larval prothoracic spiracle and the cephaloskeleton were described and figured (Deeming 1981a), while Sabrosky (1951: 737, 741) described and figured the posterior spiracle of the puparium. There is currently no identification key to Afrotropical species.

***Phyladelphus* Becker** (Chloropinae)**.** A genus of six valid species (Fig. 84), occurring in the Afrotropical, Australasian and Palaearctic Regions (Evenhuis & Pape 2020). Three species are recorded from the Afrotropics: *P. geminus* Becker, 1910 (Fig. 84), recorded from the highlands of Kenya and Ethiopia; *P. woodi* Deeming, 2018, from Zambia and Zimbabwe; and *P. maraisi* Deeming, 2018, from Namibia (Deeming 2018). Confirmatory characters include: body, legs and wings short and robust (Fig. 84); postpedicel slightly longer than deep; arista thickened and blade-like (appearing thicker due to dense microtrichia), invariably entirely black (Fig. 84); head slightly higher than long (Fig. 84); ocellar triangle bare and shiny, with pruinescent macula lateral to ocelli, triangle extending half to two-thirds length of frons, with sinuate lateral margins and linear extension to anterior margin of frons; two or more fronto-orbital setae developed on posterior part of frons; pleura largely shiny; anepisternum bare; notopleural setae 1 + 2 (Fig. 84); wing crossveins *dm–m* and *r–m* not closely approximated, separated by distance much more than length of crossvein *dm–m* (Fig. 84); anal lobe well-developed (almost a right angle) (Fig. 84); hind femur less than twice as broad as tibia; and hind tibia without tibial organ. The biology and immature stages remain unknown, but dissection of females indicated the genus is ovoviviparous (Deeming 2018). Deeming (2018) provided identification keys to Afrotropical species.

***Platycephala* Fallén** (Chloropinae)**.** A genus of 27 valid species (Fig. 85), occurring in the Afrotropical and Palaearctic Regions (Evenhuis & Pape 2020; M. von Tschirnhaus, pers. comm. 2021). The single Afrotropical species, *P. scapularum* (Fig. 85), was recorded from Niger (Deeming 2018). Confirmatory characters include: pedicel and postpedicel elongate, longer than deep; arista white and slender, with short or minute pubescence (Fig. 85); frons with anterior margin extending to anterior margin of eye; ocellar triangle occupying almost entire frons, with numerous setulae inserted in small pit-like punctures (Fig. 85); ocellar and postocellar setae absent; fronto-orbital setae very small; anepisternum and katepisternum with numerous small setulae; hind femur thickened in most species (not in *P. scapularum*), ranging from more than twice as broad as tibia to thicker than at least one other femur; tibia correspondingly curved; and hind tibial organ absent. *Platycephala scapularum* (Fig. 85) is ovoviviparous (Deeming 2018). In the Palaearctic Region, larvae of some species bore the stems of Common reed and can thus cause economic damage where the reed is grown commercially, or act as control agents where it is unwanted (B. & J.W. Ismay, pers. obs.). Grochowska (1991, 1993) described the immature stages and life cycle of the Palaearctic species *P. planifrons*.

***Polyodaspis* Duda** (Oscinellinae)**.** A genus of 19 valid species (Fig. 86), occurring in the Afrotropical, Oriental and Palaearctic Regions (Evenhuis & Pape 2020; M. von Tschirnhaus, pers. comm. 2021). Nine widely distributed species are recorded from the Afrotropics, distributed in Central, East, Southern and West Africa and the Southern Arabian Peninsula. Cherian (2012) sank *Fiebrigella* (now *Lasiambia* in the Afrotropical and Palaearctic Regions) and *Polyodaspis* as junior synonyms of *Anacamptoneurum*, but we treat these as separate genera as discussed above for *Anacamptoneurum*. Confirmatory characters include: postpedicel rounded apically; eye bare, with long axis diagonal; frons shiny (in some species dulled by microsculpture); gena broad, characteristically divided diagonally from vibrissal angle dorsally to occiput, ventral part smooth and

shiny (often with distinct setulae), dorsal part dulled (without setulae); facial carina strongly developed; ocellar setae short, reclinate and convergent; postocellar setae stout, straight and parallel, slightly reclinate; scutum densely and strongly punctured (Fig. 86); anepisternum bare, but may possess micro-sculpture; notopleural setae 1 + 3 or more, rarely appearing as 1 + 2 with dorsal posterior weaker and less distinct; scutellum disk flattened, with 7–12 pairs of lateral, stout and subequal in length scutellar setae (Fig. 86); wing crossvein *dm–m* at least slightly oblique (Fig. 86); hind tibial spur and male mid femoral organ absent; and hind tibial organ present. The biology of the genus is poorly known, but extralimital species have been recorded from a wide range of media, including other insects and plants (Ferrar 1987: 108). Large numbers of males of the Palaearctic *P. sulcicollis* (Meigen, 1838) were observed attracting females by rapid wing-waving combined with the extrusion of their abdominal vesicles (Bazyar *et al*. 2015). Deeming & Al-Dhafer (2012) illustrated the puparium and the larval cephaloskeleton of *P. picardi* and Nartshuk & Andersson (2013: 231) figured the third-instar larva, the cephaloskeleton and the spiracular zones of the southern European walnut pest species *P. ruficornis*. There is currently no identification key to Afrotropical species.

***Pselaphia* Becker** (Oscinellinae)**.** A genus of ten valid species (Fig. 87), occurring in the Afrotropical, Australasian, Palaearctic and Oriental Regions (Deeming & Al-Dhafer 2012; Ebejer & Kettani 2016; Evenhuis & Pape 2020; J.W. Ismay, pers. obs.; M. von Tschirnhaus, pers. comm. 2021). There are eight described species recorded from the Afrotropics, distributed in the Atlantic Ocean Islands, Central, East and Southern Africa and the Southern Arabian Peninsula (Dawah & Abdullah 2006; Deeming 2011: 793; Deeming & Al-Dhafer 2012; Evenhuis & Pape 2020). Numerous additional undescribed species are known from Namibia, South Africa, Yemen and Zimbabwe (Deeming & Al-Dhafer 2012 for details of specimens from Yemen). This genus is especially speciose and abundant in Southern Africa, but there remains uncertainty over the correct assignment of some species to the genus (B. Ismay, unpubl.). Confirmatory characters include: postpedicel ranging from almost round to several times as long as deep, dorsal apical corner distinctly pointed (in some species) and sexual dimorphism apparent (Deeming 2011: 793; Deeming & Al-Dhafer 2012) (Figs 17, 87); antennal foveae absent; eye pubescent (Fig. 17); ocellar triangle heavily pruinescent to shiny, not extending to anterior margin of frons; face without vertical ridge or carina; fronto-orbital setae fine (except in *P. haladai* Kubík, 2006) and evenly sized, none much larger than remainder; ocellar setae reclinate and convergent; postocellar setae convergent; scutum with setulae arranged irregularly; pleura partly shiny (Fig. 87); anepisternum pruinescent, except at posterior margin, but without setulae; notopleural setae 1 + 2; scutellum rounded, shorter than wide, without projections or tubercles; and hind tibial spur and male mid femoral organ absent, but hind tibial organ present. Biology and immature stages remain unknown. Partial identification keys to Afrotropical species were provided by Deeming & Al-Dhafer (2012) and Kubík (2006).

***Pseudochromatopterum* Deeming** (Chloropinae)**.** An endemic monotypic genus, with the single described species, *P. rileyi* Deeming, 1981 (Fig. 121), recorded from Central African Republic, Ghana and Nigeria (Deeming 1981; Evenhuis & Pape 2020). Confirmatory characters include: large (4 mm), shiny, brownish yellow species (Fig. 121); scutum and head yellow; postpedicel shorter than deep; arista white with minute whitish pubescence; head broader than thorax, with all setae and setulae black (Fig. 121); ocellar triangle bare, straight-sided, separated laterally from eye margin and reaching anterior margin of frons; gena *ca* one-quarter as deep as depth of postpedicel; occiput concave; head setae short, except longer outer vertical seta; inner vertical seta absent; ocellar setae proclinate, but short; postpronotal and prescutellar dorsocentral setae weakly developed; scutum with black presutural macula on each side; notopleural setae 1 + 1 and postalar setae strongly developed; wing membrane hyaline, with wide dark fascia along anterior margin up to and including tip (Fig. 121); halter brown; hind femur less than twice as broad as tibia; male mid femoral organ developed; and hind tibial organ more than half-length of tibia. Biology and immature stages remain unknown.

***Pseudogampsocera* Sabrosky** (Oscinellinae)**.** An endemic monotypic genus, with the single described species, *P. scutellata* (Fig. 122), confined to the Indian Ocean islands of Comoros, Mauritius and Seychelles (Evenhuis & Pape 2020). Confirmatory characters include: postpedicel reniform; arista strongly flattened laterally, long-pubescent dorsally and ventrally, inserted at apex of postpedicel (Fig. 122); eye pubescent; ocellar triangle without rows of punctures; facial carina absent; postocellar setae not parallel; inner vertical seta *ca* equal in length to postocellar seta; outer vertical seta 1.5 × length of inner; ocellar and postocellar setae erect and cruciate; pleura extensively shiny; anepisternum bare; scutellum considerably longer than wide, disc convex, with single pair of approximated apical setae developed, but margins of scutellum bearing numerous small setulae situated on tiny tubercles (Fig. 122); hind tibia without ventral apical spur; and hind tibial organ and male mid femoral organ developed, but latter minute. The immature stages have been recorded from the grass, *Stenotaphrum dimidiatum*, by Sabrosky (1964), but have not been described and the biology otherwise remains unknown.

***Pseudogaurax* Malloch** (Oscinellinae)**.** A genus of 70 valid species (Figs 88, 123), occurring in all zoogeographical regions, except Antarctica (M. von Tschirnhaus, pers. comm. 2021). There are 14 Afrotropical species, distributed in Central, East and West Africa, the Southern Arabian Peninsula, Cabo Verde and the Indian Ocean Islands. Confirmatory characters include: most species yellow, with dark fasciae on scutum and scutellum and dark marks on pleura (although some entirely black) (Figs 88, 123); antennal postpedicel reniform (in some species), or deeper than long (in many); arista inserted far from base of postpedicel and may be slender, with short pubescence to greatly broadened and flat, with dense pubescence (Figs 88, 123); eye deeper than long, pubescent (Fig. 88); ocellar triangle large, bare, smooth and shiny, occupying most of frons, reaching almost to anterior margin of frons (Fig. 123); 5–6 fronto-orbital setae fine and evenly sized, none much larger than remainder; outer vertical and postocellar setae enlarged, *ca* equal in size (Fig. 123), inner vertical setae smaller than both; pleura shiny; anepisternum bare; notopleural setae 1 + 1 or 1 + 2; scutellum usually much longer than wide (except in *P. dissimilipes*, where it is short and broadly rounded and disc strongly flattened) (Figs 88, 123); apical scutellar setae may be on tubercles and may be strongly approximated (in some

species), much longer than lateral scutellar setae (Figs 88, 123); hind tibia without apical ventral spur, but with distinct tibial organ; and male mid femoral organ absent. In the Afrotropics, larvae are known to be predators of egg masses of spiders and mantid oothecae (Boulard *et al*. 1989; Cogan 1977). Asquith & Adamski (1989) described the third-instar larva of *P. signatus* with detailed illustrations and Nartshuk & Andersson (2013: 231) figured the puparium of *P. chiyokae*. Additional biological information is available under "Economic significance" above. There is no identification key to all Afrotropical species, but Cogan (1977) provided an identification key to the Malagasy species and described some new species and Sabrosky (1945) provided an identification key to four different Afrotropical species, which was expanded on by Séguy (1951). Sabrosky (1990) provided an identification key to the then known Afrotropical species, but due to lack of material did not distinguish three species.

***Psilacrum* Becker** (Oscinellinae)**.** A genus of 20 described species (Fig. 90), occurring in all zoogeographical regions, except Antarctica (Evenhuis & Pape 2020; J.W. Ismay, pers. obs.; M. von Tschirnhaus, pers. comm. 2021). The genus was originally described from *P. giganteum* (Enderlein, 1911), from the Afrotropical Region, the only described species from the Afrotropical Region, distributed in Equatorial Guinea and Nigeria (Evenhuis & Pape 2020; Sabrosky *et al*. 1980). An additional 10 undescribed species are known from Kenya, Liberia, Nigeria and Republic of Congo and are under revision (J.W. Ismay & J.C. Deeming, unpubl.). This genus is regarded as being placed within the subfamily Oscinellinae, following Wheeler (2010: 1138) and further comments are included under "Classification" above. Confirmatory characters include: frons (in many species) with area of different micro-sculpture or pubescence to rest of frons at posterior lateral corners, close to, but outside posterior corners of ocellar triangle (Fig. 18); ocellar setae proclinate and divergent (Figs 18, 90); fronto-orbital setae fine and evenly sized, at most half as long as ocellar setae (Figs 18, 90); anepisternum bare; notopleural setae 1 + 1; wing with second costal sector, more than twice as long as third sector; vein M_1 not concave posteriorly (Figs 90, 151); hind tibia and distal 2–3 segments of hind tarsi black; hind tibial organ present; and hind tibial spur and male mid femoral organ absent. Biology and immature stages remain unknown, but in Australasia adults have been found attracted to the young shoots of the creeper Glory Vine, *Faradaya splendida* F. Muell. (Lamiaceae) (Ismay 1986). There is currently no identification key to Afrotropical species.

***Rhodesiella* Adams** (Oscinellinae)**.** A large genus of 147 valid species (Fig. 91), occurring in all zoogeographical regions, except Antarctica (Evenhuis & Pape 2020; M. von Tschirnhaus, pers. comm. 2021). The Afrotropical fauna includes 25 species, distributed in the Atlantic Ocean Islands, Central and East Africa, Indian Ocean Islands, Southern Africa, Southern Arabian Peninsula and West Africa (Deeming & Al-Dhafer 2012; Evenhuis & Pape 2020; M. von Tschirnhaus, pers. comm. 2021), but there are additional undescribed species known from Namibia, Nigeria, Kenya. This genus is regarded as being placed within the subfamily Oscinellinae, following Wheeler (2010: 1138) and further comments are included under "Classification" above. In agreement with Nartshuk (2012) this genus is regarded as being included in the tribe Rhodesiellini. Confirmatory characters include: most species black and shiny (Fig. 91); with well-developed head, thoracic and scutellar setae and very dense, but short setulae (Fig. 91); arista distinctly pubescent; eye bare, with long axis vertical; gena narrow; ocellar setae usually long, proclinate and divergent; postocellar setae as long as ocellar setae, erect and cruciate, all other head setae very long; anepisternum setulose; scutellum usually conical to subconical, narrowing more or less regularly from base to apex (shortly conical or rounded in some species), usually with single pair of apical scutellar setae and 1–2 pairs of lateral setae, without very long projections, but (in some species), with distinct tubercles at setal bases, these projections distinctly shorter than remainder of scutellum and scutellum shorter than abdomen (Figs 131, 132); wing venation characterised by vein M_1 often curving towards vein R_{4+5}, before running parallel to it; vein R_{2+3} short, so that second costal sector much shorter than third sector (Figs 91, 152); hind tibial organ and anteroventral spur absent; male mid femoral organ may be present and in some species a similar organ may be present on inner surface at base of male hind femur. *Rhodesialla formosa* has been reared from the Gassa tree in Kenya and some other species have been reared from damaged plant tissue in Papua New Guinea (J.W. Ismay, unpubl.) and twigs of Breadfruit trees in Hawaii (Ferrar 1987: 114), but the immature stages remain unknown. There is currently no recent identification key to Afrotropical species.

***Rhopalopterum* Duda** (Oscinellinae)**.** A genus of 20 valid species (Fig. 92), occurring in the Nearctic, Neotropical and Palaearctic Regions (Evenhuis & Pape 2020; M. von Tschirnhaus, pers. comm. 2021). Although the genus is not formally recorded from the Afrotropics, several undescribed species are known from Namibia. Ismay (2000: 276) tentatively recorded the genus from the Brandberg massif (Namibia's highest mountain) and this generic determination is here considered correct. The genus is very similar to *Oscinella* and additional research is required to determine the status of the two genera. Confirmatory characters include: postpedicel *ca* as long as deep; arista slender, with short microtrichia, or bare (Fig. 92); eye faintly setulose, with axis slightly deeper than long; ocellar triangle shiny, extending more than half-length of frons, without setulae within lateral margins; frons with anterior margin straight, not concave; gena with whitish pruinescence, narrower than depth of postpedicel (Fig. 92); ocellar setae reclinate and convergent; postocellar setae erect and cruciate; fronto-orbital setae fine and evenly sized, none much larger than remainder; proboscis short and fleshy; palpus small and narrow; scutum shiny, with setulae irregularly arranged (not appearing as long rows of setulae), separated by less than length of a setula; pleura extensively shiny (Fig. 92), with narrow pruinescence on dorsal margins of anepisternum and anepimeron, but the katepisternum shiny; anepisternum bare; notopleural setae 1 + 1; scutellum broader than long, thinly pruinescent (in contrast to shiny scutum), with longer pair of apical setae and smaller pair of lateral setae and a few setulae on disc; wing with second costal sector, less than 2.5 × as long as third sector (Fig. 92); and hind tibia without spur, but tibial organ present. The genus has been reared from the stems of sedges in other regions (Nartshuk & Andersson 2013: 141). Larvae of the Nearctic species *R. atriceps* (as *Stenoscinis atriceps*) have been recorded as secondary invaders of sedge stems attacked by the scathophagid *Cordilura varipes* (Valley *et al*. 1969), but the immature stages remain unknown. No identification key is currently available for Afrotropical species.

***Sabeurina* Deeming** (Chloropinae)**.** An endemic genus of two described species: *S. minuta* (Loew, 1860) (Fig. 93), recorded from Botswana, Kenya, Lesotho and South Africa (Deeming 2018; Evenhuis & Pape 2020); and *S. occidentalis* Deeming, 2018, from Nigeria (Deeming 2018). Confirmatory characters include: large species with body length *ca* 4 mm; postpedicel longer than deep; arista thin (Fig. 93); ocellar triangle bare, extended to anterior margin of frons (or virtually so) (Fig. 19); frons greatly produced anteriorly (Fig. 19); notopleural setae 1 + 2; wing vein R_{2+3} running proximally to costal vein (C) (Fig. 93); hind femur less than twice as broad as tibia (Fig. 93); and hind tibial organ and spur absent. Deeming (2018) recorded *Sabeurina* as ovoviviparous, commented briefly on the first-instar larvae, but the biology and all immature stages otherwise remain unknown. Deeming (2018) provided an identification key to the two species.

***Sabroskyina* Beschovski** (Oscinellinae)**.** A genus of three valid species occurring in the Afrotropical, Oriental and Palaearctic Regions (Dawah *et al*. 2020; Deeming & Al-Dhafer 2012; M. von Tschirnhaus, pers. comm. 2021). The two Afrotropical species are recorded as follows: *Sabroskyina aharonii* (Fig. 94), is recorded from Cabo Verde, Chad, Mali, Niger, Nigeria, Oman, Seychelles, Sudan and Yemen in the Afrotropics and *S. sinuata* from Kenya, Mali, Oman, Yemen and Zimbabwe (Dawah *et al*. 2020; Deeming & Al-Dhafer 2012). A third species was recorded by Sabrosky (1951: 824, as "*Oscinella* sp."), but was left undescribed, due to its poor condition. A female of this species in perfect condition is known from the Great Rift Valley, Kenya. Confirmatory characters include: tiny, pruinescent or shiny species, *ca* 1.5 mm in length; postpedicel *ca* as long as deep; arista slender, with short microtrichia (Fig. 94); eye bare; ocellar triangle shiny, reaching almost to anterior margin of frons (in *S. aharonii*), or two-thirds distance of frons (in *S. sinuata*) (Fig. 94); facial carina undeveloped; gena linear (in *S. sinuata*) or half depth of postpedicel (in *S. aharonii*); ocellar setae erect and convergent; postocellar setae erect and cruciate; fronto-orbital setae fine and evenly sized, none much larger than remainder; inner and outer vertical setae almost equal in size (the largest head setae in *S. aharonii*, outer vertical longer in *S. sinuata*); scutal setulae moderately numerous and irregularly arranged; pleura partially pruinescent (Fig. 94); anepisternum bare; katepisternum medially with setulae from dorsal to ventral margins and anterior and posterior margins bare; notopleural setae 1 + 1; scutellum wider than long (in *S. aharonii*), or twice as wide as long (in *S. sinuata*); apical scutellar setae longer than scutellum, more widely separated than lateral setae and in *S. sinuata* with long third seta; wing with second costal sector, less than 2.5 × as long as third sector; cell *br* broadened and in *S. sinuata* apical section of vein M_1 curved, first towards vein R_{4+5} and then away from it; hind tibia without spur, but with tibial organ; and male mid femoral organ present. Biology and immature stages remain unknown, except that *S. aharonii* feeds on the secretions from the eyes of humans (Dawah *et al*. 2020) and has been recorded swarming in masses in and around Sudanese houses (Lewis 1954: 76; Sabrosky 1949: 61). Deeming & Al-Dhafer (2012) provided an identification key to Afrotropical species.

***Scoliophthalmus* Becker** (Oscinellinae)**.** A genus of 22 shiny black valid species (Fig. 95), occurring in the Afrotropical, Australasian, Oriental and Palaearctic Regions (Evenhuis & Pape 2020; M. von Tschirnhaus, pers. comm. 2021). Seven species are recorded from the Afrotropics, distributed in Central and East Africa, Indian Ocean Islands, Southern Africa, Southern Arabian Peninsula and West Africa (Deeming & Al-Dhafer 2012; Evenhuis & Pape 2020). Confirmatory characters include: arista bare; eye bare, longer than deep, with long axis more or less diagonal (Fig. 95); ocellar triangle long, bare, smooth and shiny black, reaching anterior margin of frons; facial carina low, only developed between antennal bases; gena broad, produced anteriorly, but rounded, highly polished, with surface glabrous, without microtrichia, setulae or setae, but with a few setulae on dorsal margin and row on ventral margin (Fig. 95); ocellar setae proclinate and widely divergent (Fig. 95); postocellar setae erect and cruciate; fronto-orbital setae *ca* 10, becoming longer posteriorly; pleura shiny; anepisternum with numerous setulae (Fig. 95); notopleural setae 1 + 2, the anterior slightly smaller; scutellum shorter than scutum, conical to subconical, narrowing more or less regularly from base to apex, distinctly shorter than abdomen, usually with single pair of apical setae and 1–2 pairs of lateral setae; wing (in two species) with costal vein (C) extending almost to vein M_1, but with distinct gap distally (Fig. 95); hind tibial organ and spur absent; male mid femoral organ developed into patch of small setulae; and male terminalia of *S. trapezoides* with postgonites long and base of distiphallus heavily sclerotised. Species have been reared from many species of grasses and cereal crops, including as primary invaders of Maize, millet, rice, Sugarcane and Sorghum and in some cases as secondary invaders after attacks by other species, but the immature stages remain unknown (Anonymous 1969; Dawah *et al*. 2020; Deeming 1972: 7; Deeming & Al-Dhafer 2012). Deeming (2006) provided an identification key, which included six Afrotropical species and Deeming & Al-Dhafer (2012) provided an identification key to the species occurring in the Arabian Peninsula, including a newly described species.

***Semaranga* Becker** (Chloropinae)**.** A genus of two valid species (Fig. 96), occurring in the Afrotropical, Australasian, Oriental and Palaearctic Regions (Cherian 2016; Evenhuis & Pape 2020; M. von Tschirnhaus, pers. comm. 2021). The yellow species, *S. dorsocentralis* Becker, 1911 was recorded in the Afrotropics from the Atlantic Ocean Islands, East and Southern Africa, Southern Arabian Peninsula and West Africa (Deeming & Al-Dhafer 2012; Evenhuis & Pape 2020). *Semaranga* was synonymised under *Elachiptereicus* by Nartshuk (2013) and Riccardi & Amorim (2020), but Cherian (2016) described a second species and the genus is here retained pending further research. Confirmatory characters include: postpedicel reniform; arista blade-like, thickened and densely pubescent (Fig. 96); ocellar triangle bare, extending to anterior margin of frons; ocellar setae short, proclinate and divergent; postocellar setae divergent and shorter; fronto-orbital setae *ca* three small setae; pleura shiny; anepisternum bare; postpronotal seta undeveloped; notopleural setae 1 + 2; three pairs of large, black dorsocentral setae, anterior pair presutural (Fig. 96); wing crossveins *dm–m* and *r–m* closely approximated, separated by distance much less than length of vein *dm–m*; veins R_{2+3} and R_{4+5} not curved towards costal vein (C); hind femur less than twice as broad as tibia; indistinct, narrow hind tibial organ present; and male terminalia with postgonites long, bearing two long, strong black setae. Biology and immature stages remain unknown.

***Sepsidoscinis* Hendel** (Oscinellinae)**.** Currently a genus with two described species, *S. maculipennis* Hendel, 1914 and *S. niger* Cherian, 2012 (Fig. 97), known from the Oriental Region (M. von Tschirnhaus, pers. comm. 2021). One undescribed species is known from the Afrotropics, from Rwanda. Confirmatory characters include: postpedicel rounded; arista thin and short-pubescent; eye large, oblique, with short, sparse setulae (Fig. 97); ocellar triangle large and shiny, almost reaching anterior margin of frons, with line of setulae along outside margin; gena narrow (Fig. 97); ocellar setae minute, proclinate and convergent; postocellar setae minute and cruciate; scutum shiny, without long, erect setae, but evenly clothed in pale setulae (Fig. 97); pleura shiny; prothorax expanded into neck-like structure, between head and thorax, with distinct dorsal transverse carina (Fig. 97); notopleural setae 1 + 1; scutellum broader than long, flattened and pruinescent, without long, erect setae, with scutellar setae inserted on short tubercles (Fig. 97); wing narrow and banded; veins R_{2+3} and R_{4+5} curved towards anterior margin (Fig. 97); hind tibial organ present, but male femoral organ absent; and abdominal synsternite 1 + 2 elongate and narrow. Biology and immature stages remain unknown.

***Siphlus* Loew** (Chloropinae)**.** A genus of two valid species (Fig. 98), occurring in the Afrotropical and Oriental Regions (Evenhuis & Pape 2020). *Siphlus vittatus* (Wiedemann, 1830) is recorded from South Africa and Zimbabwe (in the Afrotropics) and *S. seminifer* Sabrosky, 1951 (Fig. 98) from Nigeria and Zambia (J.C. Deeming, pers. obs.; Evenhuis & Pape 2020). Confirmatory characters include: robust species (Fig. 98), 4.0–5.5 mm in length, up to 2 mm broad; body very deep and head much deeper than long; postpedicel at most 1.25 × as long as deep; arista not thickened and flattened (Fig. 98); ocellar triangle reaching almost to anterior margin of frons, with more than one row of minute setulae within lateral margins in posterior part; gena very broad, broader than eye is deep, with setulae arising from small seed-like swellings over most of surface (Fig. 98); ocellar, postocellar, fronto-orbital and vertical setae all undeveloped; scutum, katepisternum and scutellum with small, seed-like swellings at bases of setulae; notopleural setae minute 1 + 1; scutellum with 5–6 pairs of tiny, stout, black setae on enlarged bases low down on apex; wing membrane hyaline; crossveins *dm–m* and *r–m* separated by distance much greater than length of crossvein *dm–m* (Fig. 98); hind femur less than 2 × as broad as tibia; hind tibia uniformly clothed in minute setulae, with narrow tibial organ; and without male mid femoral organ. Biology and immature stages remain unknown. The two described species can be distinguished using Sabrosky (1951: 734).

***Siphonella* Macquart** (Oscinellinae)**.** A genus of three valid species (Fig. 99), occurring in the Afrotropical, Australasian, Nearctic, Oriental and Palaearctic Regions (Evenhuis & Pape 2020; M. von Tschirnhaus, pers. comm. 2021; Nartshuk 2012). A single Afrotropical species, *S. perlonga* Becker, 1913, is known from the region, recorded from Ethiopia. Confirmatory characters include: eye with long axis not strongly diagonal; ocellar triangle shiny, with single row of punctures and setulae within each lateral margin; facial carina distinctly developed, separating bases of antenna and continuing ventrally to lower facial margin; antennal foveae concave; postocellar setae erect and convergent, or slightly reclinate; ocellar setae short, slightly reclinate and convergent; proboscis long (including labella) and geniculate (Figs 20, 99); pleura mostly shiny (Fig. 99); anepisternum bare; scutellum short and broadly rounded apically; wing vein R_{2+3} relatively long; second costal sector, equal to, or longer than, third sector (Fig. 99); hind tibia without apical or subapical spur, but with distinct tibial organ; and male mid femoral organ slightly raised, with numerous irregular setae. In the Palaearctic, the immature stages have been found associated with spider egg masses (Ferrar 1987: 114), but Nartshuk & Andersson (2013: 145) considered this to be incorrect and recorded larvae feeding on coccids (Hemiptera: Sternorrhyncha) on grasses. In the United States, four adults were reared at the end of August from a spider egg-sac (Coquillett 1898: 75). The immature stages otherwise have not been described and there is currently no identification key to world species.

***Siphunculina* Rondani** (Oscinellinae)**.** A genus of 39 valid species (Fig. 124), occurring in the Afrotropical, Australasian, Nearctic, Oriental and Palaearctic Regions (Evenhuis & Pape 2020; M. von Tschirnhaus, pers. comm. 2021). Eleven species have been recorded from the Afrotropical Region, distributed in the Atlantic Ocean Islands, Central and East Africa, Indian Ocean Islands, Southern Africa, Southern Arabian Peninsula and West Africa (Deeming & Al-Dhafer 2012; Evenhuis & Pape 2020) and there are numerous undescribed species known from Namibia, Nigeria and South Africa. Confirmatory characters include: head and thoracic setae greatly reduced; postpedicel short and round (Fig. 124); eye usually bare or at most with minute, sparse pubescence; ocellar triangle extending to anterior margin of frons, with single row of small setulae within lateral margins (Fig. 124); facial carina strongly developed, broadened at dorsal and ventral margins, separating deep antennal foveae; gena produced anteriorly; ocellar and postocellar setae erect and convergent; fronto-orbital setae *ca* 6 equal-sized; proboscis short; scutum clothed in minute, irregularly arranged setulae, except along acrostichal and dorsocentral lines, where one row of setulae is more regularly arranged (Fig. 124); pleura partly shiny; anepisternum bare, but may have posterodorsal patch of minute pilosity; notopleural setae 1 + 1 or 1 + 2; postpronotal seta indistinct; scutellum shorter than long, with short (shorter than scutellum) apical setae; wing (in most species) with second costal sector much shorter than third, as vein R_{2+3} short (Fig. 124), but in Afrotropical *S. lobeliaphila* Sabrosky, 1951, *S. loici* Nartshuk, 2001, *S. lurida* Enderlein, 1911 and *S. matilei* Nartshuk, 2001, vein R_{2+3} much longer and second sector more equal in length to third; then apical scutellar setae less than half-length of scutellum; in other characters, including very short scutellum and scutellar setae, species agree with the other *Siphunculina* and are best retained in that genus; halter black in at least some species; hind tibia without spur, but with oval tibial organ; and the male mid femoral organ absent. Species have been reared from mammal and bird dung and droppings and adults are eye gnats, attracted to human and animal eyes in the Australasian and Oriental Regions and in Egypt, being implicated in the transmission of diseases of humans and other mammals, including livestock; the adults have also been reported from wounds. The immature stages have not been described. Nartshuk (2001) and Sabrosky (1951: 773) provided partial identification keys to Afrotropical species.

***Speccafrons* Sabrosky** (Oscinellinae)**.** A genus of eight valid species (Fig. 100), occurring in the Afrotropical, Nearctic, Oriental and Palaearctic Regions (Evenhuis & Pape 2020; Liu & Yang 2015; M. von Tschirnhaus, pers. comm. 2021). One species, *S. araneolicida* (Lamb, 1937), is known from Mauritius (J.W. Ismay, unpubl.) and an undescribed species is known from Cameroon and Nigeria, but the latter species does not have the surstylus enlarged and requires further work. Confirmatory characters include: postpedicel *ca* as long as deep; arista slender with microtrichia (Fig. 21); eye clothed in short, but distinct microtrichia (Fig. 21); ocellar triangle pruinescent; frons grey with small setulae set in darker maculae (Fig. 21); facial carina narrow and low, extending to oral margin; gena smoothly rounded, not projecting and narrower than depth of postpedicel; ocellar setae reclinate and convergent; postocellar setae reclinate and cruciate; fronto-orbital setae fine and evenly sized, none much larger than remainder; pleura mostly shiny (Fig. 100), pruinescent only on dorsal margin of anepisternum; anepimeron and anepisternum bare; notopleural setae 1 + 2; scutellum shorter than broad and rounded, with setulae extending over lateral margin of scutellum, marginal setae not inserted on distinct tubercles (Fig. 137); hind tibia without spur, but with broad tibial organ; male mid femoral organ present; and male terminalia with large, shiny black, globular surstylus (often visible without dissection). Some species have been reared from spider egg masses (Nartshuk & Andersson 2013: 148), but the immature stages have not been described. Certain Oriental species aggregate in masses on hanging cords (M. von Tschirnhaus, pers. comm. 2021). A recent revision by Liu & Yang (2015) included an identification key to world species.

***Steleocerellus* Frey** (Chloropinae). A genus of 15 valid species (Figs 101), occurring in the Afrotropical, Australasian and Oriental Regions (Evenhuis & Pape 2020; M. von Tschirnhaus, pers. comm. 2021). There are eight Afrotropical species, recorded from East, Central, Southern and West Africa and the Southern Arabian Peninsula (Deeming & Al-Dhafer 2012; Evenhuis & Pape 2020). Confirmatory characters include: body, legs and wings more or less narrowly elongate (Fig. 101); postpedicel with straight dorsal margin; arista entirely black and thickened, usually flattened and blade-like (or appearing thickened due to dense microtrichia) (Fig. 101); head longer than deep; ocellar setae proclinate; postocellar setae proclinate and slightly divergent (much smaller than ocellar setae); two fronto-orbital setae developed; thorax shiny (at least on pleura); anepisternum bare; thoracic setation well-developed (Fig. 101); postpronotal setae developed; notopleural setae 1 + 2; strong dorsocentral seta present; wing crossveins *dm–m* and *r–m* not closely approximated, with cell *dm–m* elongate; anal lobe undeveloped; hind femur less than twice as broad as tibia; fore tarsus not laterally compressed (Fig. 101); hind tibial organ long and narrow; and hind tibia without apical spur. The immature stages have been found in grasses and cereal crops (Deeming & Al-Dhafer 2012). Kirk-Spriggs (1986) provided detailed descriptions of the puparia, including the cephaloskeleton of three species. Sabrosky (1951: 724) provided identification keys to some of the species (as *Mepachymerus*).

***Stenophthalmus* Becker** (Chloropinae)**.** A genus of four valid species (Fig. 102), occurring in the Afrotropical, Oriental and Palaearctic Regions (Deeming & Al-Dhafer 2012). Three species are recorded from the Afrotropics (Deeming & Al-Dhafer 2012): *S. ocellatus* (Fig. 102), from Nigeria, Oman, Sudan and Yemen; *S. occidentalis* from Gambia, Kenya, Nigeria, Oman, Senegal and Yemen; and *S. typhae* Nartshuk, 1971 from Oman. Confirmatory characters include: yellow species with black markings (Fig. 102); postpedicel slightly acuminate at anterodorsal corner (except in *S. typhae* where this tapers to a sharp point); arista white (Fig. 102); ocellar triangle narrow and pruinescent, extending *ca* two-thirds length of frons; fronto-orbital setae reduced to 3–4 slightly enlarged pairs; proboscis short; pleura pruinescent (Fig. 102); anepisternum bare; notopleural setae 1 + 1 or 1 + 2; wing marked in one species (*S. occidentalis*); hind femur less than twice as broad as tibia; hind tibia uniformly setulose, without discrete tibial organ and tibial spur; and male terminalia with surstylus at least partially fused to epandrium. The immature stages have been reared from the shoots of cultivated Maize, millets, Sorghum, Sugarcane and grasses (Deeming & Al-Dhafer 2012) and Deeming & Al-Dhafer (2012) described the puparium and illustrated the cephaloskeleton of *S. occidentalis*, but their biology remains unclear. Deeming & Al-Dhafer (2012) provided an identification key to species.

***Stenoscinis* Malloch** (Oscinellinae)**.** A genus of 13 valid species (Figs 103, 104), occurring in all zoogeographical regions, except the Palaearctic Region and Antarctica (Evenhuis & Pape 2020; J.W. Ismay, unpubl.). Four species are recorded from the Afrotropics, distributed in East, Southern and West Africa (Evenhuis & Pape 2020) and at least one additional undescribed species is known from Kenya. The genus is regarded as being placed within the subfamily Oscinellinae, following Wheeler (2010: 1138) and further comments are included under "Classification" above. Confirmatory characters include: body, wings and legs long and narrow (Figs 103, 104); eye large and bare, with posterior margin slightly excavated (Fig. 104); ocellar triangle very large and shiny, occupying almost all of frons; gena linear (Fig. 104); ocellar setae small, but proclinate (in some species); inner vertical setae large and proclinate; postocellar setae small and proclinate; remaining head setation reduced in size; scutum with sparse setulae arranged in long rows, with bare areas between; pleura shiny (Figs 103, 104); anepisternum bare; wing appearing petiolate due to reduction or absence of anal lobe, but alula present but very small (Figs 103, 104); membrane strongly marked in one species (*S. submarginifusca* Sabrosky, 1951); hind tibia without apical spur, but with well-developed tibial organ and male mid femoral organ absent. In Nigeria, *S. arnos* has been reared from shoots of Southern cut grass (J.C. Deeming, unpubl.), which is a serious weed pest of rice and a pest of Maize and Sugarcane (CABI 2020). Immature stages have not been described. Sabrosky (1951: 809) provided an identification key to all described Afrotropical species.

***Strobliola* Czerny** (Oscinellinae)**.** A genus of six valid species (Fig. 105), occurring in the Afrotropical, Australasian, Oriental and Palaearctic Regions (Evenhuis & Pape 2020; Ismay 1998). Ismay (1998) synonymised the better known *Aprometopis* with this genus and Deeming & Al-Dhafer (2012) followed this, although *Strobliola* was erroneously treated as a junior synonym in the world checklist of chloropid genera (Nartshuk 2012). Two yellow species are recorded from the Afrotropics: *S. flavofacies* (Fig. 105), from East and Southern Africa, Southern Arabian Peninsula and West Africa (Deeming & Al-Dhafer

2012; Evenhuis & Pape 2020); and *S. minima* (Lamb, 1918), from Oman (Deeming & Al-Dhafer 2012; Ismay 1998) and at least one additional undescribed species is known from Nigeria. Confirmatory characters include: antennae small (Fig. 105); postpedicel short and rounded; antennal foveae deeply concave (Fig. 22); eye with long axis strongly diagonal; head elongate, distinctly longer than high (Fig. 105); frons densely setulose, unusually broad, twice width of eye; ocellar triangle scarcely developed, pruinescent (as on remainder of frons); facial carina distinctly developed and broad, separating bases of antennae and continuing ventrally to lower facial margin (Fig. 22); vibrissal angle projecting beyond anterior margin of eye (Fig. 105); head and thoracic setae strong, slightly thickened; ocellar setae reclinate and parallel to convergent; postocellar setae parallel to convergent; fronto-orbital setae more than six, small and reclinate; anepisternum and anepimeron with large, shiny areas in ventral half (in some species) (Fig. 105); anepisternum bare (Fig. 105); notopleural setae 1 + 1; wing cell *br* broad (Fig. 105); hind tibia with well-developed tibial organ, but without apical spur; and male mid femoral organ expressed as patch of setae. The immature stages have been recorded from grasses and cereal crops, including Maize, millets, Sorghum, Sugarcane and Wheat (Deeming 1972: 21; Deeming & Al-Dhafer 2012; Ismay 1998; Kanmiya 1983: 151). Deeming & Al-Dhafer (2012) described and illustrated the puparium of *S. flavofacies* and Ismay (1998) described part of the puparium. Deeming & Al-Dhafer (2012) provided an identification key to species occurring in the Arabian Peninsula and Ismay (1998) provided an identification key to World species.

***Thaumatomyia* Zenker** (Chloropinae)**.** A genus of 40 valid species (Fig. 125), occurring in all zoogeographical regions, except Antarctica (Evenhuis & Pape 2020; M. von Tschirnhaus, pers. comm. 2021; Nartshuk 2000*a*). Five species are recorded from the Afrotropics, distributed in East and Southern Africa and in Yemen in the Southern Arabian Peninsula (Evenhuis & Pape 2020). Confirmatory characters include: postpedicel at most 1.25 times as long as deep; arista pubescent, but not thickened or flattened (Fig. 125); ocellar triangle extending to anterior margin of frons (in most species), with at least one row of setulae within lateral margins (Fig. 125); gena less than 0.5 × depth of postpedicel; scutellum flattened dorsally, lateral margin angled, with numerous setulae on disc (in most species); apical scutellar setae strongly approximated (Fig. 125); hind femur less than twice as broad as tibia; hind tibia with discrete tibial organ; and male abdomen with eversible sacs in lateral membranes (in some species). Larvae of extralimital species are predatory on Hemiptera: Sternorrhyncha (Ferrar 1987: 107) and Balachowsky & Mesnil (1935: 976) illustrated the larva, the larval head and the posterior spiracle of *T. glabra*. There is currently no identification key to Afrotropical species.

***Trachysiphonella* Enderlein** (Oscinellinae)**.** A genus of six valid species (Fig. 106), occurring in the Afrotropical and Palaearctic Regions (M. von Tschirnhaus, pers. comm. 2021). Three described species are recorded from the Afrotropics: *T. carinifacies* Nartshuk, 1964, from Oman, United Arab Emirates and Yemen; *T. dawahi* Deeming & Al-Dhafer, 2012, from Oman and Yemen; and *T. recurva* Deeming & Al-Dhafer, 2012, from Oman and United Arab Emirates (Deeming & Al-Dhafer 2012) and additional undescribed species are known from Namibia. There is some confusion over the correct name for the genus, as some workers assumed that Sabrosky (1980*b*) synonymised *Trachysiphonella* under *Dasyopa* Malloch, while Nartshuk (2012), in the world checklist retained *Trachysiphonella*, but Cherian & Jyothi (2015) applied *Dasyopa* in their revision of the Indian species. *Trachysiphonella* is here retained, until such time as the position is clarified. Confirmatory characters include: mostly small species (< 2 mm); body colour yellow with darker markings (Fig. 106); antenna not elongate; postpedicel about as long as deep; arista slender (Fig. 106); eye pubescent; ocellar triangle pruinescent, indistinct and reduced in size (scarcely larger than ocellar tubercle) (Fig. 106); vibrissal angle produced anteriorly to oral margin (Fig. 106); facial carina well-developed, separating deep antennal foveae; ocellar and postocellar setae erect and convergent; fronto-orbital setae fine and uniformly sized; proboscis elongate and geniculate; pleura partly pruinescent (Fig. 106); anepisternum bare; notopleural setae 1 + 2; apical scutellar setae widely separated basally; hind tibia with long tibial organ, but without tibial spur; and male mid femoral organ distinct. Adults of extralimital species have been recorded in participating in the ant-meal of a spider (Harkness & Ismay 1975), or as obligatory pollinators of Apocynaceae or Birthwort (*Aristolochia* species) (Oelschlägel *et al*. 2014), but the immature stages remain unknown. Deeming & Al-Dhafer (2012) provided an identification key to species occurring in the Arabian Peninsula.

***Trichieurina* Duda** (Chloropinae)**.** A genus of four valid species (Fig. 107), occurring in the Afrotropical and Palaearctic Regions (Evenhuis & Pape 2020). Two species occur in the Afrotropics: *T. haladai* Kubík & Barták, 2014, described from Zambia; and *T. sabroskyi* Stuckenberg, 1982, from Malawi (Kubík & Barták 2014) (Evenhuis & Pape 2020). Confirmatory characters include: postpedicel longer than deep; arista thin (Fig. 107); head longer than deep (Fig. 107); head and thorax clothed in dense, long setulae, most of which are longer than length of postpedicel (Figs 23, 107); ocellar triangle large, extending to anterior margin of frons (Fig. 23); frons with anterior margin considerably produced anterior to eye (Fig. 23); ocellar setae small and erect; outer vertical setae slightly longer than head setulae; inner vertical setae shorter; fronto-orbital setae not longer than head setulae; notopleural setae indistinguishable from setulae; hind tibial organ and spur absent; and hind femur less than twice as broad as tibia. Biology and immature stages remain unknown. Kubík & Barták (2014) provided a re-description of the genus and an identification key to world species.

***Tricimba* Lioy** (Oscinellinae)**.** A genus of 181 valid species (Fig. 126), occurring in all zoogeographical regions, except Antarctica (M. von Tschirnhaus, pers. comm. 2021). Eleven widespread species are known from the Afrotropics, distributed in Central and East Africa, Indian Ocean Islands and Southern Africa (Evenhuis & Pape 2020; M. von Tschirnhaus, pers. comm. 2021), but there are numerous additional undescribed species known from Kenya, Namibia and South Africa. Confirmatory characters include: postpedicel shorter than deep or as long as deep; eye either entirely bare or (in some species), densely pilose; facial carina well-developed (in many species); gena varying from retracted to strongly projecting anteriorly; ocellar setae erect to slightly reclinate; head and thoracic setae greatly thickened and enlarged (in Afrotropical species); scutum with median and dorsocentral lines with deeply incised rows of punctures (Fig. 126); pleura partially shiny, at least

anepisternum, anepimeron or katepisternum with extensive shiny area; anepisternum bare; notopleural setae 0 + 1, 1 + 1 or 1 + 2; scutellum either arched, with scutellar setae enlarged, inserted on tubercles (Fig. 126), or shorter and flatter than broad, with setae not inserted on tubercles; hind tibial organ well-developed, but without apical or subapical spur or one spur shorter than diameter of tibia in Afrotropical species and male mid femoral organ developed in some species. Larvae of extralimital species have been recorded from a variety of media, including decaying vegetable matter, fungi and the egg masses of spiders (Ferrar 1987: 115; Ismay 1993). Ferrar (1987: 616, 619, 620, 622) illustrated the third-instar larva and details of the puparium of the Australian species *T. steatodae* (now *T. convexa* Malloch, 1927 (Ismay 1993)) and Ismay (1993) figured the puparium, cephaloskeleton and posterior spiracles of the puparium of *T. cardamomi*. Sabrosky (1951: 777) provided a partial identification key to Afrotropical species.

Undescribed genus A (Oscinellinae)**.** This undescribed genus includes 19 species (Fig. 108) and occurs in the Afrotropical, Australasian and Oriental Regions. Two undescribed species are recorded from the Afrotropics, one from South Africa and one from Mauritius. Confirmatory characters include: postpedicel as long as deep (Figs 24, 108); ocellar triangle either conspicuous and large, or small and poorly differentiated, shiny or pruinescent (Fig. 24); ocellar setae proclinate and slightly convergent (Fig. 24); postocellar setae cruciate to inclinate; posterior fronto-orbital seta longer than several other enlarged upper fronto-orbital setae (Fig. 24); anepisternum bare; notopleural setae 1 + 1, the anterior larger; wing cell *br* distinctly broadened medially where veins R_{2+3} and R_{4+5} divide (Fig. 108); hind tibial organ well-developed, but spur absent; and male mid femoral organ present (in some species). The biology and immature stages remain unknown. The new genus is currently under description (J.W. Ismay, in prep.).

Undescribed genus B (Oscinellinae)**.** This undescribed genus (Fig. 109) is represented by one Afrotropical species from Kenya, which cannot be attributed to any described genus. Confirmatory characters include: postpedicel as long as deep; head elongate, distinctly longer than high (Fig. 109); eye with long axis somewhat diagonal; frons *ca* twice width of eye; ocellar triangle pruinescent, extending half-length of frons; vibrissal angle distinctly produced in front of eye margin (Fig. 109); facial carina strongly developed; most head and thoracic setae thickened and white; ocellar setae tiny, erect and convergent; postocellar setae erect and convergent; anepisternum and anepimeron almost entirely pruinescent, with only minute shiny area on ventral margins (Fig. 109); notopleural setae 1 + 2 (Fig. 109); and hind tibial organ present, but indistinct, but tibial spur absent. It has been reared from bat guano in association with *Mormotomyia hirsuta* Austen, 1936 (Mormotomyiidae) from Ukasi Hill, Kenya (A.H. Kirk-Spriggs, pers. comm. 2020), but the immature stages remain unknown.

Undescribed genus C (Oscinellinae)**.** This undescribed genus (Fig. 110) is represented by one undescribed species from Katima Mulilo, Namibia and Morogoro, Tanzania. It cannot be placed in any existing genus without expanding the generic concepts and is here left undescribed pending further studies of relationships. Confirmatory characters include: postpedicel not reniform, *ca* as deep as long (Fig. 25); arista blade-like and thickened, with dense microtrichia (Figs 25, 110); ocellar triangle small, slightly pruinescent, extending *ca* half-length of frons (Fig. 25); ocellar setae inserted outside ocellar tubercle, erect and long, at least as long as outer vertical setae; postocellar setae erect and cruciate; fronto-orbital setae equally sized; apical scutellar setae long, widely separated basally, not inserted on tubercles; pleura at least partly shiny (Fig. 110); notopleural setae damaged and cannot be described; wing with first costal sector, subequal to, or shorter than, second sector; crossvein *r–m* positioned in basal half of wing (Fig. 110); and hind tibial organ elongate, covering *ca* one-third of tibia, but hind tibial spur absent. Biology and immature stages remain unknown.

Undescribed genus D (Chloropinae)**.** This undescribed genus is represented by one female specimen from Côte d'Ivoire (M. von Tschirnhaus, pers. comm. 2010), which does not fit in any described genus and cannot be described until further material is available. Confirmatory characters include: large yellow species (> 5 mm), black only on maculae lateral to ocelli and at tip of ocellar triangle; postpedicel shorter than deep, with apex darkened; arista not thickened and flattened; gena more than 0.5 × depth of eye; scutellum flattened on disc and lateral margin angled; apical scutellar setae strongly approximated; wing crossveins *dm–m* and *r–m* not closely approximated, separated by distance greater than length of vein *dm–m*; hind femur less than twice as broad as tibia; and hind tibial organ distinct. Biology and immature stages remain unknown.

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CHYROMYIDAE 97

(Golden-eyed Flies)

Martin J. Ebejer

Fig. 97.1. Male of *Gymnochiromyia nigrimana* (Malloch) (non-Afrotropical) (photograph © S.A. Marshall).

Diagnosis

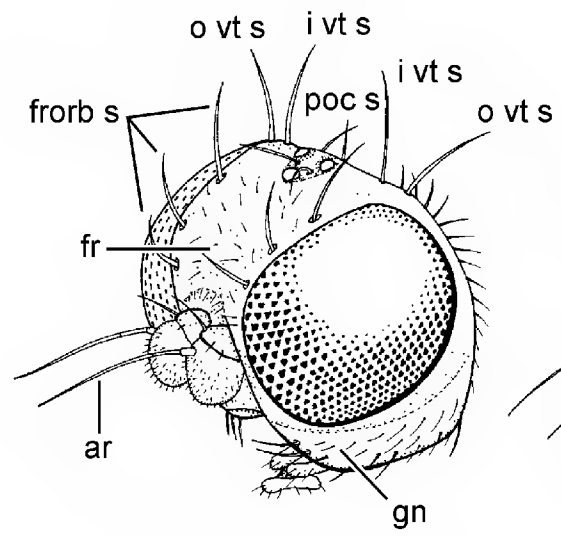
Minute- to small-sized acalyptrate flies (body length: 0.75–4.5 mm), the majority with pale yellow integument and vestiture of setae and setulae generally well-developed (Fig. 1).

Head (Figs 2–9) with eyes iridescent in all species, generally bright green in living flies (Fig. 1), sometimes purple to reddish brown; eye facets enlarged at extreme anterior angle adjacent to antennae, smallest facets at posterior extremity of eye, facets of intermediate area gradually diminishing in size from anterior to posterior; without top to bottom demarcation line; ocelli invariably set in small equilateral triangle at vertex (e.g., Fig. 3); 1 pair of proclinate, usually divergent, ocellar setae (or setulae) positioned more or less medially on ocellar triangle (e.g., Fig. 3) (in a few *Aphaniosoma* Becker species these setae may be parallel); antenna (Figs 10–13) short, with round pedicel; arista 3-articled in Chyromyinae and *Krifomyia* Ebejer; 2-articled in *Aphaniosoma*, *Paraphaniosoma* Ebejer (Fig. 12) and *Tethysimyia* Ebejer (Fig. 13); in Chyromyinae (Figs 2–5), with 3 strong fronto-orbital setae, the anterior inclinate; in Aphaniosominae (Figs 6–9) with 0–6 reclinate fronto-orbital setae; strong inner and outer vertical setae present; short, parallel or cruciate postocellar setae usually present.

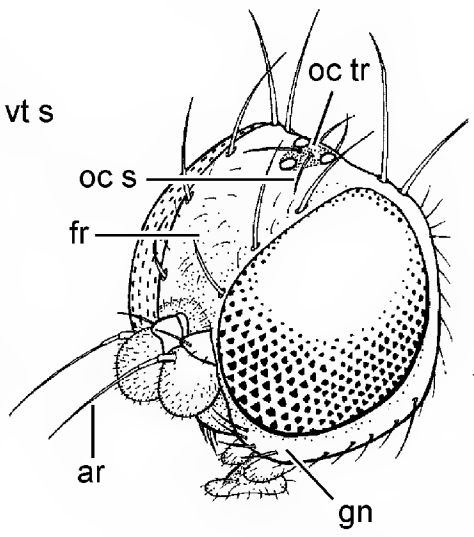
Thorax with scutum usually thinly pale pruinose; gently convex from anterior to posterior, without prescutellar depression (Figs 34–41); pleura (Figs 42, 43) with 1 anepisternal seta at hind margin, at middle in Chyromyinae and in dorsal ⅓ in Aphaniosominae, 1 katepisternal seta inserted posterodorsally; Aphaniosominae with 1 minute propleural setula; subscutellum membranous above; scutum (Figs 34–41) with 1, rarely 2, postpronotal setae, 1 presutural seta, 1 short medially directed intra-postpronotal seta in Aphaniosominae (except *Krifomyia*

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2021. Manual of Afrotropical Diptera. Volume 3. Brachycera—Cyclorrhapha, excluding Calyptratae. *Suricata* 8. South African National Biodiversity Institute, Pretoria; pp. 2115–2130.

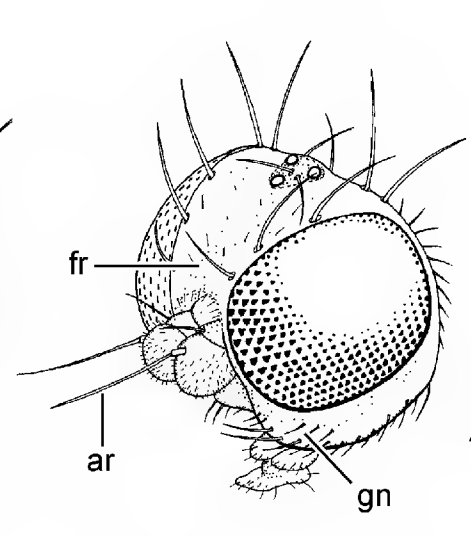
and *Tethysimyia*); 2 notopleural setae; 0–1 prealar seta, 1 supra-alar seta, 1 postalar seta, 0–3 + 3–8 dorsocentral setae, hindmost present and strong; acrostichal setae differentiated from scutal setulae or not, in 2 to 10 rows, 1–2 pairs of strong prescutellar setae sometimes present, *Oroschyromya* Ebejer (Fig. 36) with 1 strong intrapostalar seta; halter pale. Scutellum usually with 2 pairs of scutellar setae (Figs 34, 36–41), but 3 pairs in *Notiochyromya* Ebejer (Fig. 35); only *Somatiosoma* Frey (Fig. 37) with discal scutellar setulae. Wing (e.g., Fig. 17) uniformly microtrichose hyaline (with diffuse infuscation across middle of wing in only one species); costagial break at subcostal vein (*Sc*); humeral crossvein (Figs 17–25) variable, from small thin translucent vein (little more than a fold), to broad thick-set vein; costal vein (*C*) complete or weakened at humeral crossvein in Chyromyinae (Figs 17–21); invariably broken just beyond humeral crossvein in Aphaniosominae (Figs 22–25); vein R_1 short; subcostal vein (*Sc*) complete, joining costal vein at vein R_1 (e.g., Fig. 17); vein R_{2+3} slightly and symmetrically arcuate, gradually



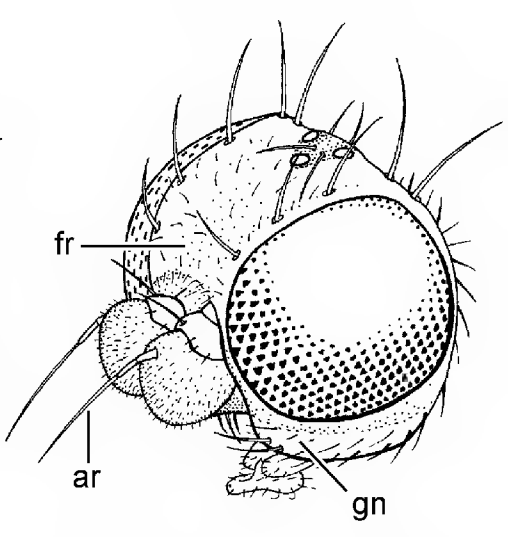
2 *Gymnochiromyia*



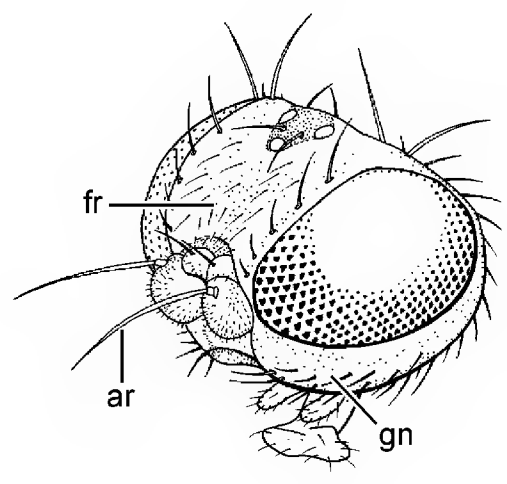
3 *Notiochyromya*



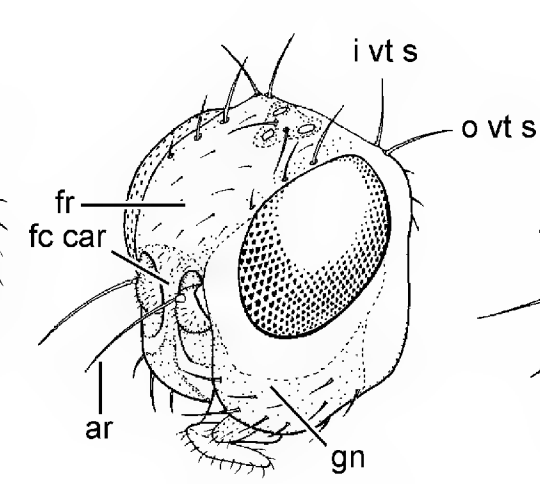
4 *Oroschyromya*



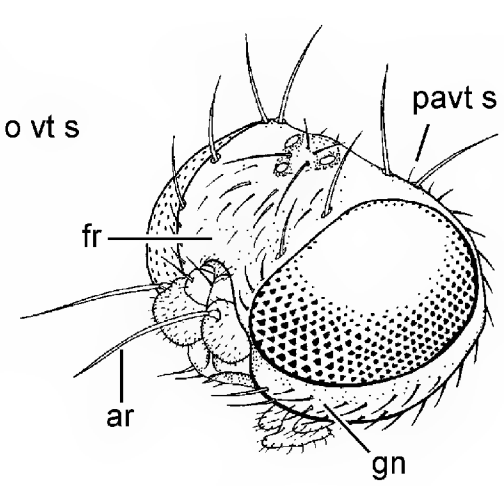
5 *Somatiosoma*



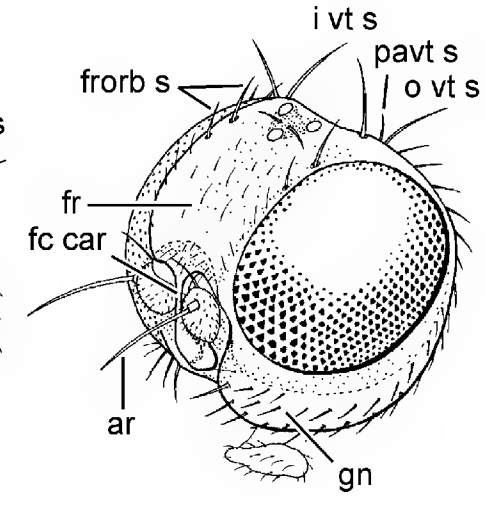
6 *Aphaniosoma*



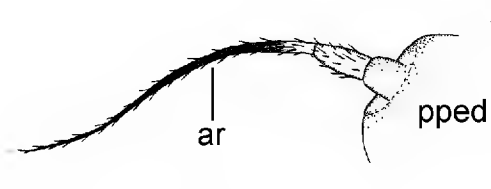
7 *Krifomyia*



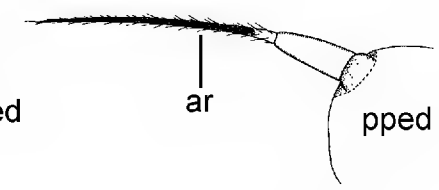
8 *Paraphaniosoma*



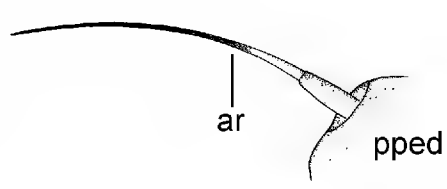
9 *Tethysimyia*



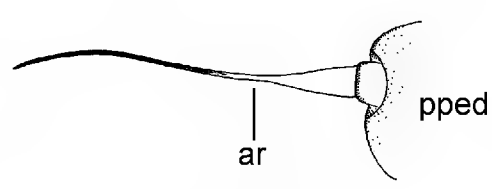
10 *Oroschyromya*



11 *Somatiosoma*



12 *Paraphaniosoma*



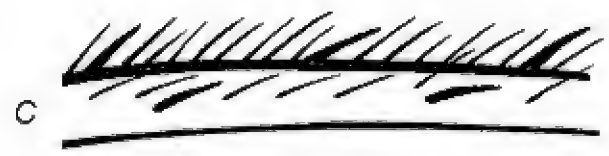
13 *Tethysimyia*

Figs 97.2–13. Heads and antennae of Chyromyidae: (2) head of *Gymnochiromyia punctata* Ebejer, anterolateral view; (3) same, *Notiochyromya monticola* Ebejer; (4) same, *Oroschyromya elongata* Ebejer; (5) same, *Somatiosoma grandicorne* Ebejer; (6) same, *Aphaniosoma conspicuum* Ebejer; (7) same, *Krifomyia minutissima* (Bezzi); (8) same, *Paraphaniosoma sexvittatum* (Lamb); (9) same, *Tethysimyia deemingi* (Ebejer); (10) antenna of *O. affinis* Ebejer, lateral view; (11) same, *S. messumensis* Ebejer; (12) same, *P. sexvittatum*; (13) same, *T. deemingi* (Ebejer). Figs 10–13 (Ebejer 2009, figs 1e, c, g, h, respectively).

Abbreviations: ar – arista; fc car – facial carina; fr – frons; frorb s – fronto-orbital seta; gn – gena; i vt s – inner vertical seta; o vt s – outer vertical seta; oc s – ocellar seta; oc tr – ocellar triangle; pavt s – paravertical seta; poc s – postocellar seta; pped – postpedicel.

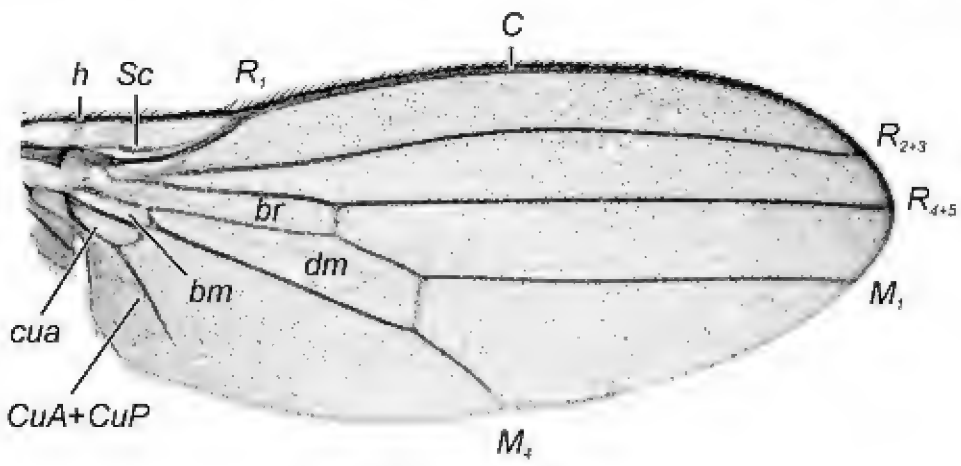
converging towards vein R_{4+5} apically (e.g., Fig. 17); veins R_{4+5} and M_1 parallel, or slightly convergent, except in *Aphaniosoma*, in which distinctly divergent (Fig. 22); costal vein tapers away after vein R_{4+5}, ending either some distance before, or just beyond apex of vein M_1; anterior margin of costal vein (*C*) setulose (Figs 14–16), usually densely so, with dark spine-like setulae interspersed among fine setulae between apices of veins R_1 and R_{2+3}; in *Krifomyia* and *Tethysimyia* costal setulae often spinose (Figs 14, 23, 25); in most Chyromyinae, spine-like setulae also on dorsal aspect of costal vein (Figs 15, 19–21); discal medial

14 *Krifomyia*

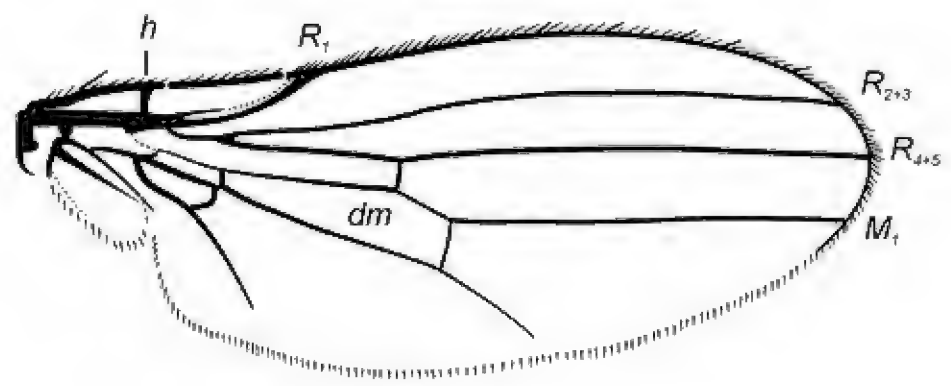


15 *Oroschyromya*

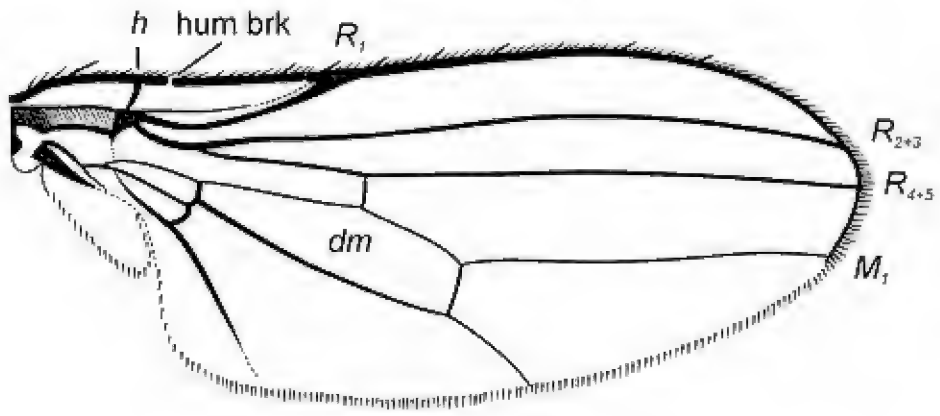
16 *Aphaniosoma*



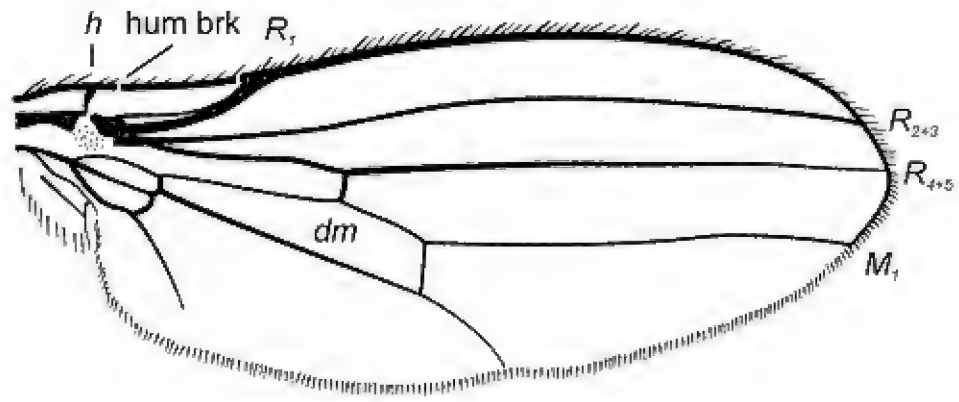
17 *Oroschyromya*



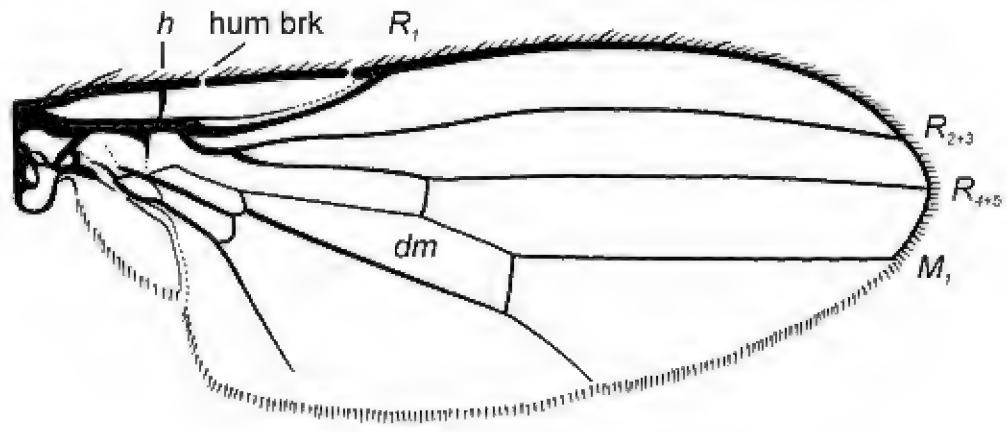
18 *Gymnochiromyia*



19 *Notiochyromya*



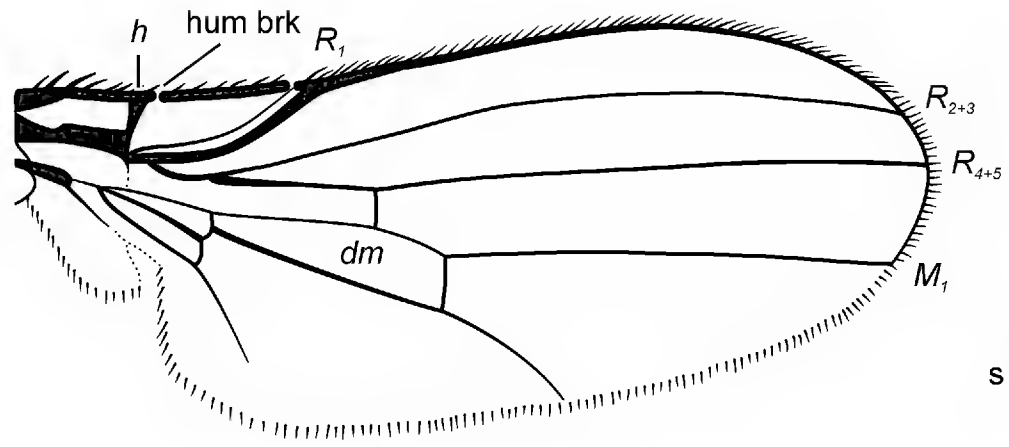
20 *Oroschyromya*



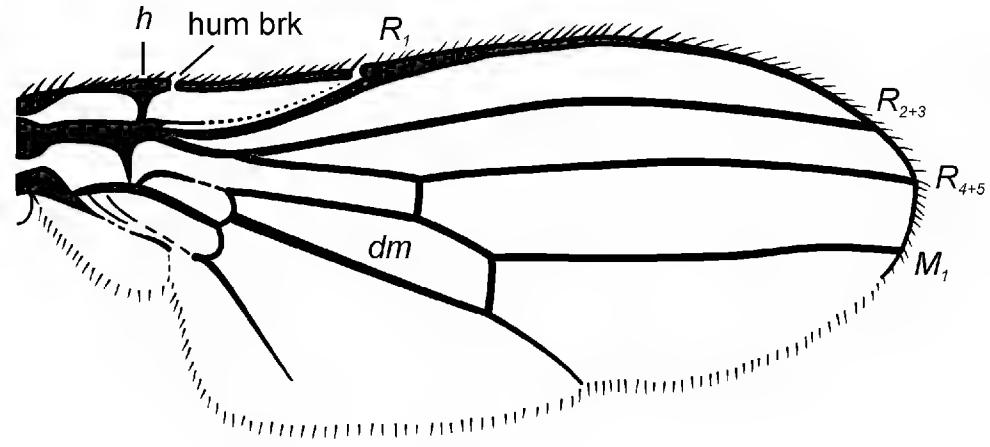
21 *Somatiosoma*

Figs 97.14–21. Anterior costal margin (distal to vein R_1) and wings of Chyromyidae (dorsal views): (14) costal margin of *Krifomyia minutissima* (Bezzi); (15) same, *Oroschyromya affinis* Ebejer; (16) same, *Aphaniosoma fissum* Collin; (17) wing of *Oroschyromya elongata* Ebejer; (18) same, *Gymnochiromyia fallax* Ebejer (non-Afrotropical); (19) same, *Notiochyromya sexspinosa* (Lamb); (20) same, *O. bicolor* Ebejer; (21) same, *Somatiosoma eremicolum* Ebejer. Figs 17–19, 21 (Ebejer 2009, figs 2g, c, e, i, respectively).

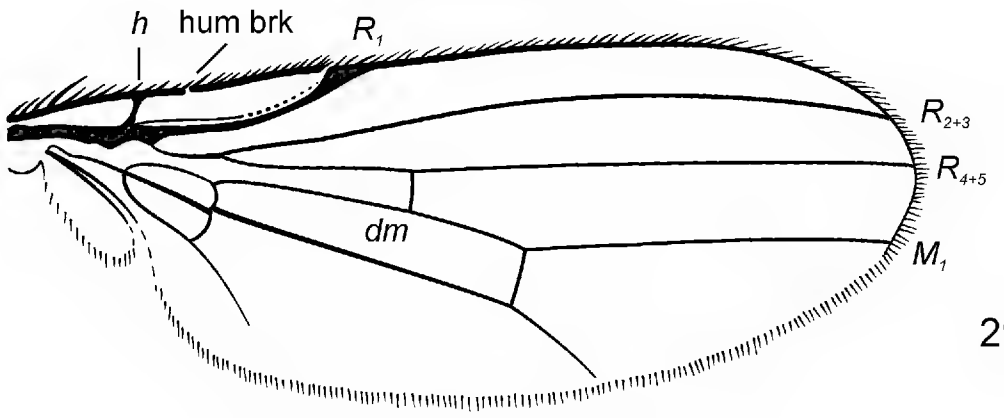
Abbreviations: *bm* – basal medial cell; *br* – basal radial cell; *C* – costal vein; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *dm* – discal medial cell; *h* – humeral crossvein; hum brk – humeral break; M_1 – first branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *Sc* – subcostal vein.



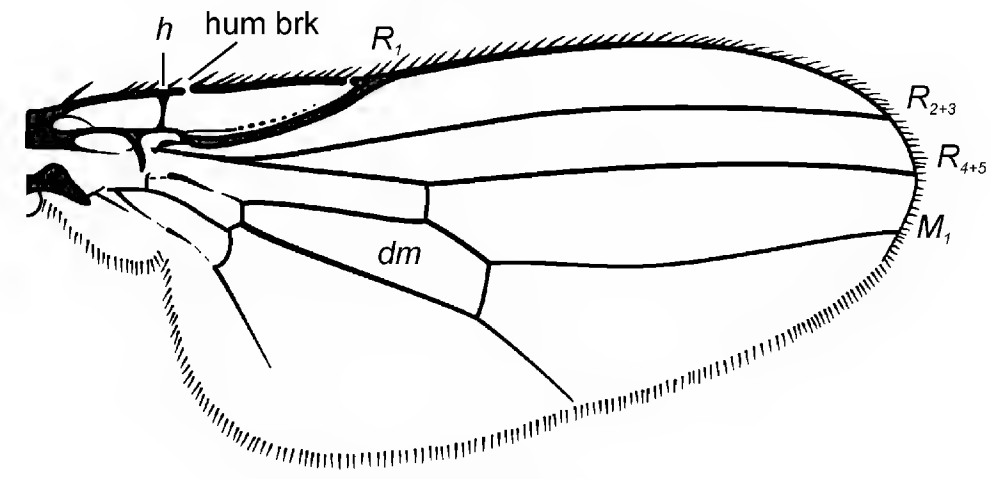
22 *Aphaniosoma*



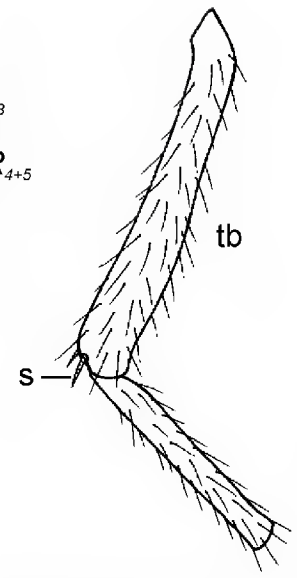
23 *Krifomyia*



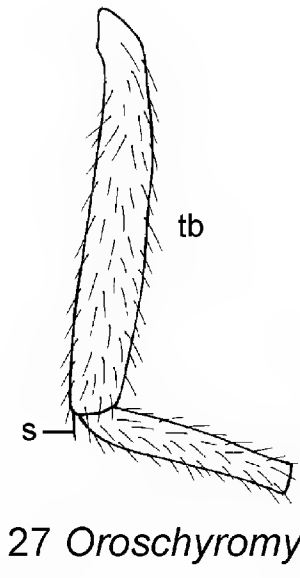
24 *Paraphaniosoma*



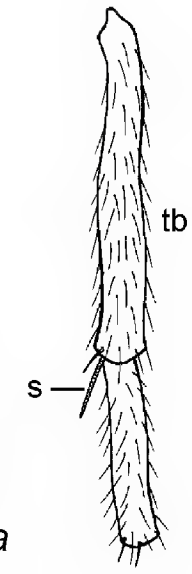
25 *Tethysimyia*



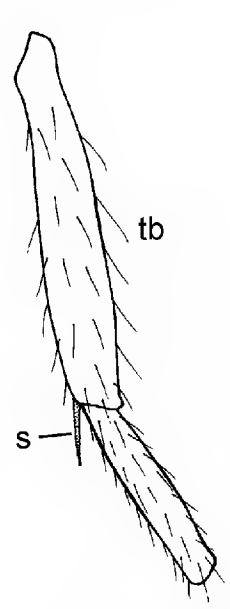
26 *Gymnochiromyia*

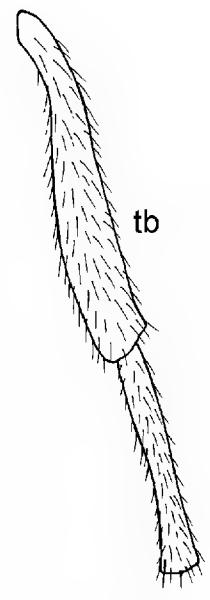


27 *Oroschyromya*

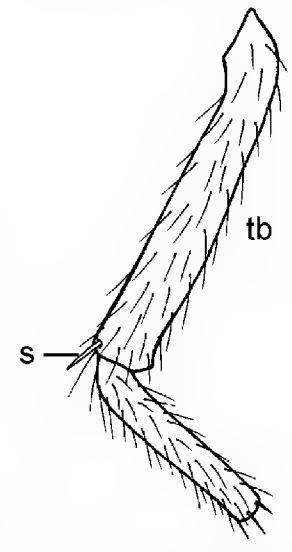


28 *Aphaniosoma*



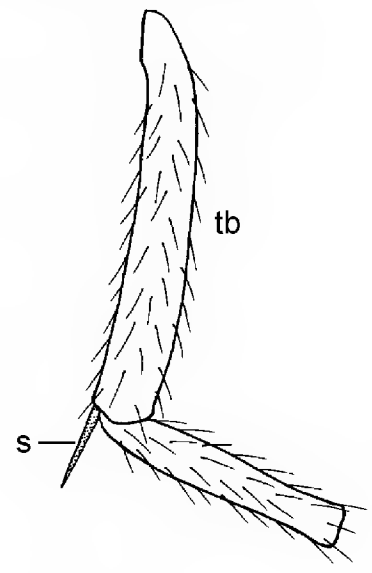


30 *Notiochyromya*

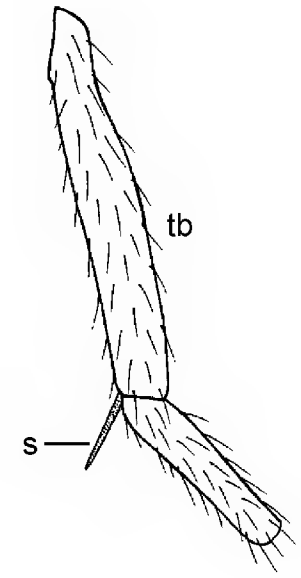


31 *Somatiosoma*

29 *Paraphaniosoma*



32 *Tethysimyia*



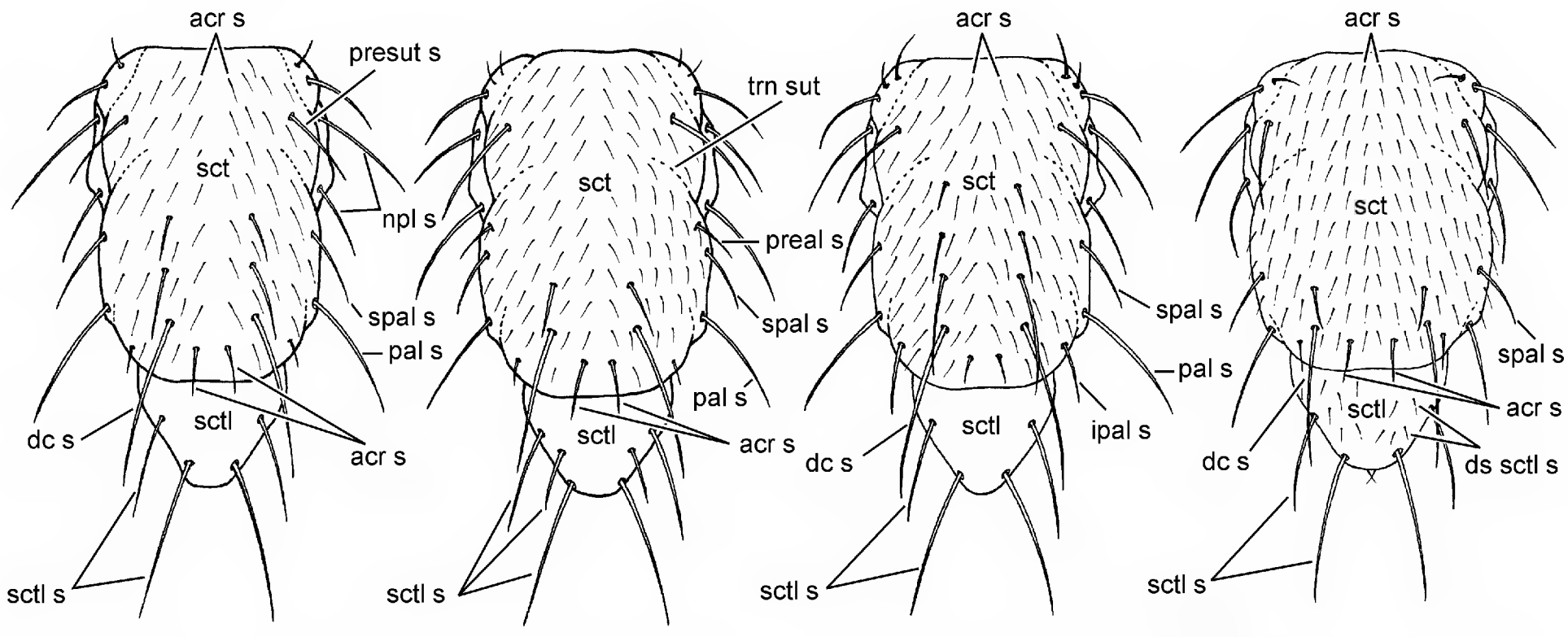
33 *Krifomyia*

Figs 97.22–33. Wings (dorsal views) and mid tibia and tarsomere 1 of Chyromyidae: (22) wing of *Aphaniosoma fissum* Collin; (23) same, *Krifomyia minutissima* (Bezzi); (24) same, *Paraphaniosoma sexvittatum* (Lamb); (25) same, *Tethysimyia deemingi* (Ebejer); (26) mid tibia and tarsomere 1 of *Gymnochiromyia megacephala* Ebejer, lateral view; (27) same, *Oroschyromya elongata* Ebejer; (28) same, *A. fissum*; (29) same, *P. sexvittaum*; (30) same, *Notiochyromya* sp. undescribed; (31) same, *Somatiosoma nitescens* Frey; (32) same, *T. deemingi*; (33) same, *K. minutissima*. Figs 22, 23, 25 (after Ebejer 2009, figs 3a, c, e).

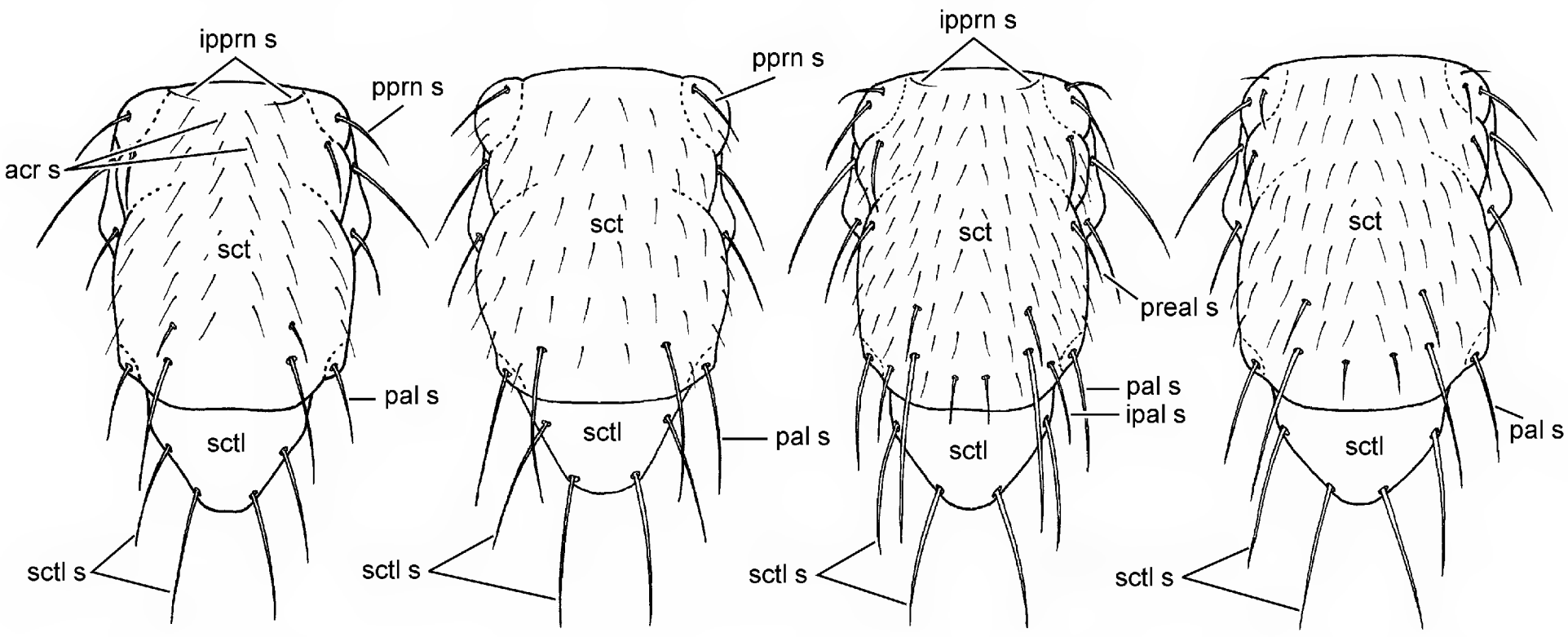
Abbreviations: *dm* – discal medial cell; *h* – humeral crossvein; hum brk – humeral break; M_1 – first branch of media; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; s – seta; tb – tibia.

cell (*dm*) more or less reaching middle of wing; cells *br* and *bm* separate; cell *cua* small and vein *CuA+CuP* not reaching wing margin (e.g., Fig. 17). Legs with femora sometimes markedly dilated in *Chyromya* Robineau-Desvoidy (non-Afrotropical), slightly so in a few species of other genera of Chyromyinae; legs of other genera with few other modifications (Figs 26–33); setae weak and setulae uniformly distributed; Aphaniosominae with long apicoventral seta on mid tibia (Figs 28, 29, 32, 33), absent or markedly reduced in Chyromyinae (Figs 26, 27, 30, 31).

Abdomen of male (Fig. 44) with 6 and female with 7 segments; in *Aphaniosoma,* male often with segments 4–6 highly modified; many species of all genera with transverse darker yellow or dark brown to black fascia on each segment; sternites weakly sclerotised to membranous; segments with fine



34 *Gymnochiromyia* 35 *Notiochyromya* 36 *Oroschyromya* 37 *Somatiosoma*



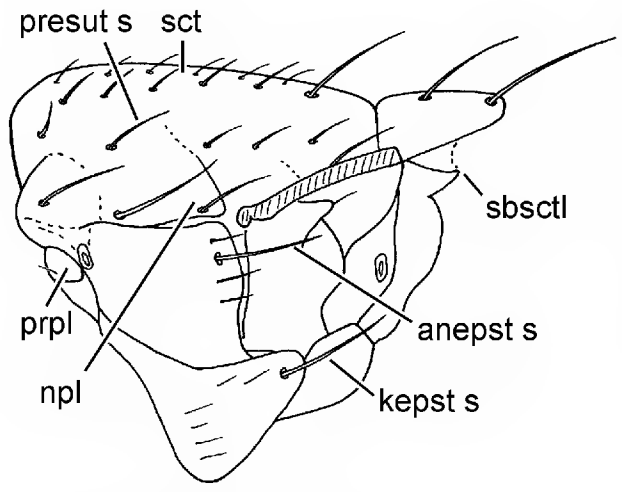
38 *Aphaniosoma* 39 *Krifomyia* 40 *Paraphaniosoma* 41 *Tethysimyia*

Figs 97.34–41. Thoraces of Chyromyidae (dorsal views): (34) *Gymnochiromyia megacephala* Ebejer; (35) *Notiochyromya monticola* Ebejer; (36) *Oroschyromya peruncinata* Ebejer; (37) *Somatiosoma nitescens* Frey; (38) *Aphaniosoma gallagheri* Ebejer; (39) *Krifomyia minutissima* (Bezzi); (40) *Paraphaniosoma sexvittatum* (Lamb); (41) *Tethysimyia deemingi* (Ebejer).

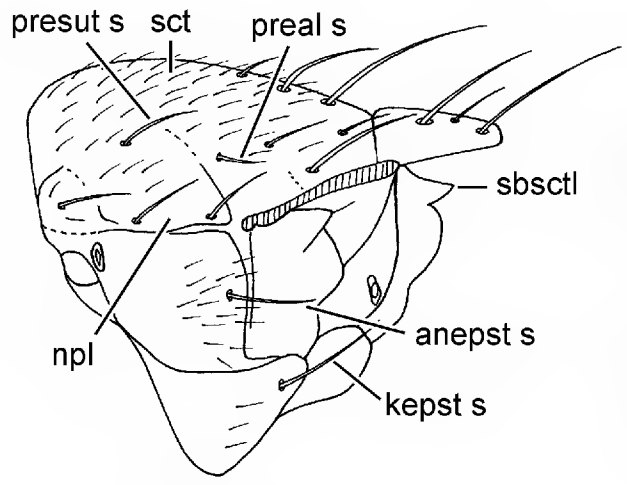
Abbreviations: acr s – acrostichal setae; dc s – dorsocentral seta; ds sctl s – discal scutellar seta; ipal s – intrapostalar seta; ipprn s – intra-postpronotal seta; npl s – notopleural seta; pal s – postalar seta; presut s – presutural seta; pprn s – postpronotal seta; preal s – prealar seta; sct – scutum; sctl – scutellum; sctl s – scutellar setae; spal s – supra-alar seta; trn sut – transverse suture.

discal and marginal setulae; male postabdomen highly modified in Aphaniosominae (Figs 65–67, 68, 71–75, 78, 79, 82, 84–86), often including secondary sexual characters from segment 5; in *Aphaniosoma*, epandrial/hypandrial complex usually invaginated, to a greater or lesser extent, within tergite 6; less so in other genera; in Chyromyinae (Figs 44, 45, 50, 57), tergite 6 distinct and epandrium external and large, with hypandrial complex enclosed within it; virtually all species of all genera with distinct surstylus and pre- and postgonite, these structures often highly modified in Aphaniosominae; phallic structures generally large and complex; cerci distinct and in *Oroschyromya*, often with modified setae; female postabdomen (Figs 46, 47, 51–56, 59–64, 69, 70, 76, 77, 80, 81, 83, 87, 88) with two spermathecae, often easily discernible, owing to very dark pigmentation; spermathecal ducts often translucent and, rarely, sclerotised in part (Figs 54, 56); tergite 7 and sternite 8 often divided; in some *Oroschyromya* species (Figs 62–64) with divided and modified tergite 6; epiproct not differentiated; hypoproct small, at most thinly sclerotised; cerci invariably small and fine setulose, except in male *Oroschyromya*, in which cerci typically enlarged, setose or spinose (Fig. 57).

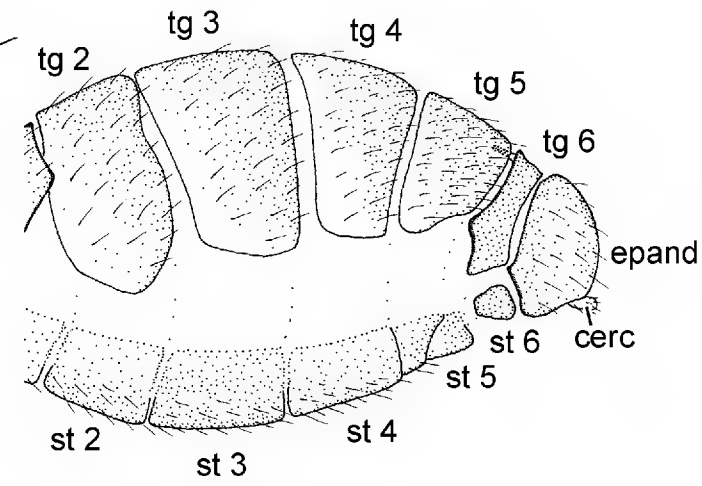
Chyromyidae are superficially similar to a number of small yellow species of acalyptrate flies in other families, most commonly in the Chloropidae (see Chapter 96). Chloropidae usually possess a large frontal triangle and a propleural carina. Other families sometimes mistaken for Chyromyidae include the Lauxaniidae (see Chapter 74) and Canacidae (Tethininae) (see Chapter 94). Chaetotaxic head characters easily separate these. In addition, the combination of absent dorsal preapical seta on the hind tibia, absence of true vibrissae and wing veins



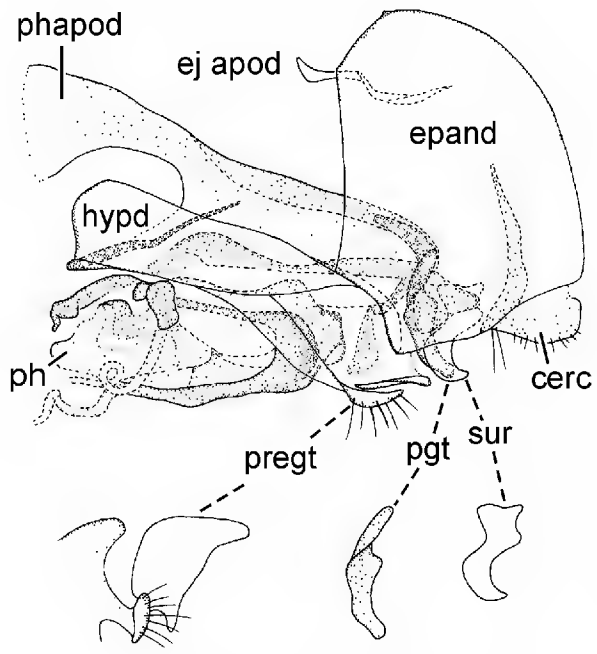
42 *Aphaniosoma*



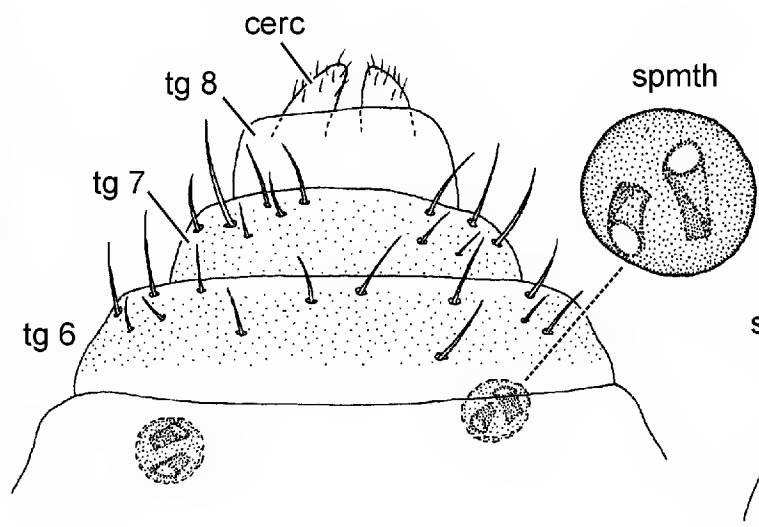
43 *Notiochyromya*



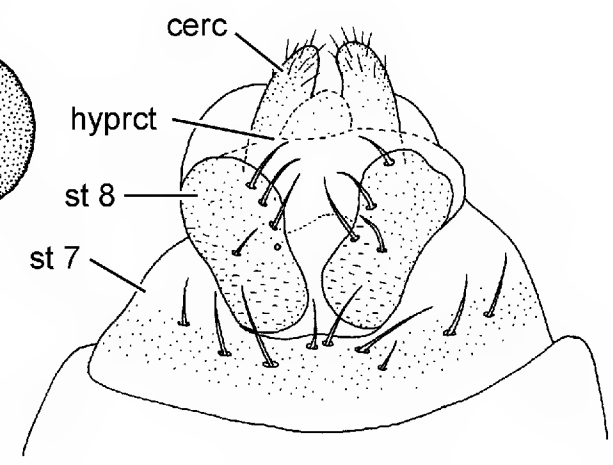
44 *Somatiosoma* ♂



45 *Somatiosoma* ♂



46 *Somatiosoma* ♀



47 *Somatiosoma* ♀

Figs 97.42–47. Thoraces, abdomens and terminalia of Chyromyidae: (42) thorax of *Aphaniosoma fissum* Collin, lateral view; (43) same, *Notiochyromya sexspinosa* (Lamb); (44) male abdomen of *Somatiosoma nitescens* Frey, lateral view; (45) same, male terminalia; (46) same, female terminalia, dorsal view; (47) same, ventral view. Figs 45–47 (Ebejer 2009, figs 28a, b, 28e, g, f, respectively).

Abbreviations: anepst s – anepisternal seta; cerc – cercus; ej apod – ejaculatory apodeme; epand – epandrium; hypd – hypandrium; hyprct – hypoproct; kepst s – katepisternal seta; npl – notopleuron; pgt – postgonite; ph – phallus; phapod – phallapodeme; preal s – prealar seta; pregt – pregonite; presut s – presutural seta; prpl – propleuron; sbsctl – subscutellum; sct – scutum; spmth – spermatheca; st – sternite; sur – surstylus; tg – tergite.

R_{2+3} and R_{4+5} gradually convergent towards the wing apex serve to separate this family from similar looking acalyptrate flies.

Biology and immature stages

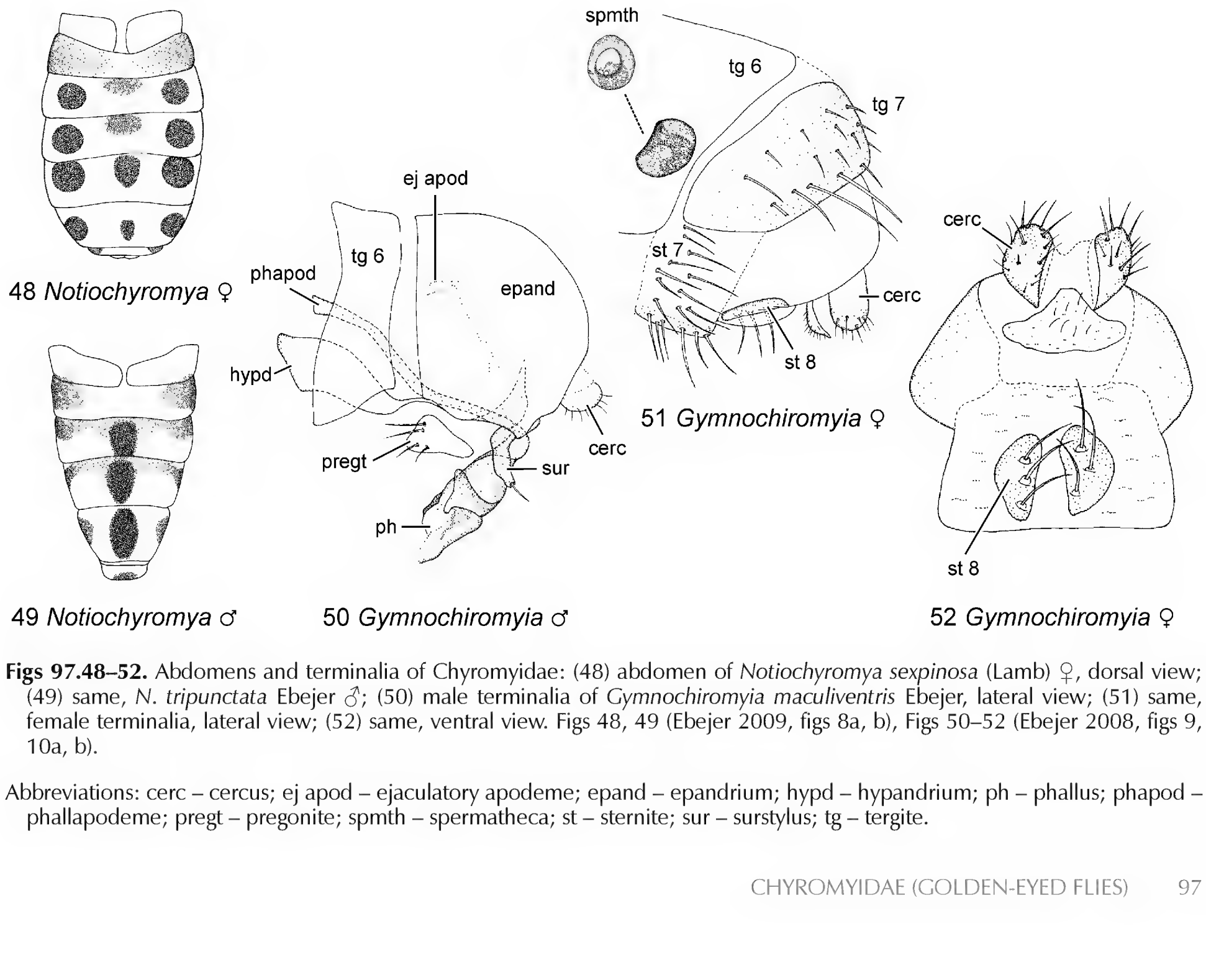
The biology and ecology of the Chyromyidae remain poorly understood; the little that is known having been summarised by Ebejer (2009) and Ferrar (1987: 121). In the Palaearctic Region, species of *Chyromya* and *Gymnochiromyia* Hendel have been reared from debris in the hollows of trees, from mammal nests and burrows and from birds' nests (Collin 1933; Rotheray 1989). *Chyromya* is also recorded as having been reared from bat guano (Smith 1989: 95). *Aphaniosoma sensu stricto* was reared from leaf litter beneath *Salicornia* (Amaranthaceae) and *Phragmites* (Poaceae) (Ebejer 1996) and from a rodent nest (Ebejer & Deeming 1997).

Rotheray (1989) tabulated E.B. Basden's records of families of Diptera reared from 19 of 106 studied birds' nests and mammal burrows and nests in Britain. *Chyromya flava* (L., 1758) was recorded from the nest of the European hedgehog, *Erinaceus europaeus* L. (Erinaceidae) and from European rabbit, *Oryctolagus cuniculus* (L.) (Leporidae) burrows and *Gymnochiromyia inermis* (Collin, 1933) from drays of Eastern grey squirrel, *Sciurus carolinensis* Gmelin and Red squirrel, *S. vulgaris* L. (Sciuridae). From birds' nests only 2.29% of individuals were Chyromyidae, reared from 12 of 228 nests of 48 species and all of the reared Chyromyidae represented *G. inermis*.

Larval feeding habits are unknown. From the location and circumstances in which puparia have been found, it may be assumed that larvae graze on decaying organic matter, the micro-habitat probably being as significant as the larval food source itself. Most records, at least in so far as they refer to *Chyromya* and *Gymnochiromyia*, suggest that larvae require the droppings of vertebrates. There are records, however, that indicate that this may not be true for all species in the family. Chandler (1973) and Cogan (1978), for example, recorded the rearing of *Gymnochiromyia* from decaying Marram grass, *Ammophila* spp. (Poaceae) and elm wood debris.

The only published descriptions of immature stages are of the puparia (with associated cephaloskeletons) of *Aphaniosoma* (Fig. 91) (Ebejer & Deeming 1997), *Chyromya* (Fig. 93) (Gibbs 2007; Rotheray 2011) and *Gymnochiromyia* (Fig. 92) (Deeming 1998), all from the Palaearctic Region.

Adults are usually encountered when sweeping vegetation with a fine-meshed hand net in suitable habitats, such as vegetated coastal dunes, grasses and Tamarisk trees, *Tamarix* spp. (Tamaricaceae), near salt marshes, and sometimes sweeping lower branches of trees along broadleaved woodland edges.



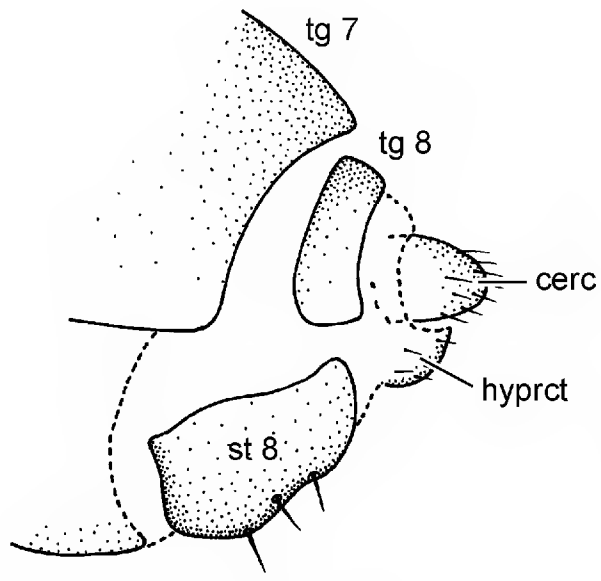
Figs 97.48–52. Abdomens and terminalia of Chyromyidae: (48) abdomen of *Notiochyromya sexpinosa* (Lamb) ♀, dorsal view; (49) same, *N. tripunctata* Ebejer ♂; (50) male terminalia of *Gymnochiromyia maculiventris* Ebejer, lateral view; (51) same, female terminalia, lateral view; (52) same, ventral view. Figs 48, 49 (Ebejer 2009, figs 8a, b), Figs 50–52 (Ebejer 2008, figs 9, 10a, b).

Abbreviations: cerc – cercus; ej apod – ejaculatory apodeme; epand – epandrium; hypd – hypandrium; ph – phallus; phapod – phallapodeme; pregt – pregonite; spmth – spermatheca; st – sternite; sur – surstylus; tg – tergite.

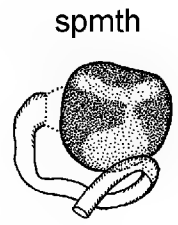
They can also be collected, often in vast numbers, in pan traps and Malaise traps. Some species, particularly *Aphaniosoma* species, frequently come to light. Adults are occasionally observed at flowers, including those of *Convolvulus* (Convolvulaceae) and *Matricaria* (Asteraceae) (Collin 1949), *Hibiscus* (Malvaceae) (Colless & McAlpine 1970), *Ipomoea* (Convolvulaceae) (Wheeler & Sinclair 1994), *Euphorbia* (Euphorbiaceae), *Foeniculum* (Apiaceae) and *Tamarix* (Ebejer 1996).

Chyromyidae are active throughout the year in hot regions of the world. In temperate regions the general preference is for hot and/or dry seasons. Thus, April to October is the main flight period in the Northern Hemisphere; conversely, in Southern Africa, it is October to March. In general, preferred habitats for the family comprise vegetated areas near still, saline or fresh water bodies within hot dry areas, or along the coast. There are exceptions, however. *Aphaniosoma socium* Collin, 1949, for example, is a north European species that appears to favour damp, regenerating landfill sites and old open mines (Bährmann 2006; Ebejer *et al*. 2001). *Chyromya* species are generally associated with broadleaved woodland or savanna, *Notiochyromya* with tropical moist forest and *Oroschyromya* with less mesic, but montane forest. A study of *Aphaniosoma* from central Asia (Ebejer 2006) has shown that long cold winters and high elevations (2,000–3,000 m) do not represent barriers to a diverse and rich fauna of Chyromyidae.

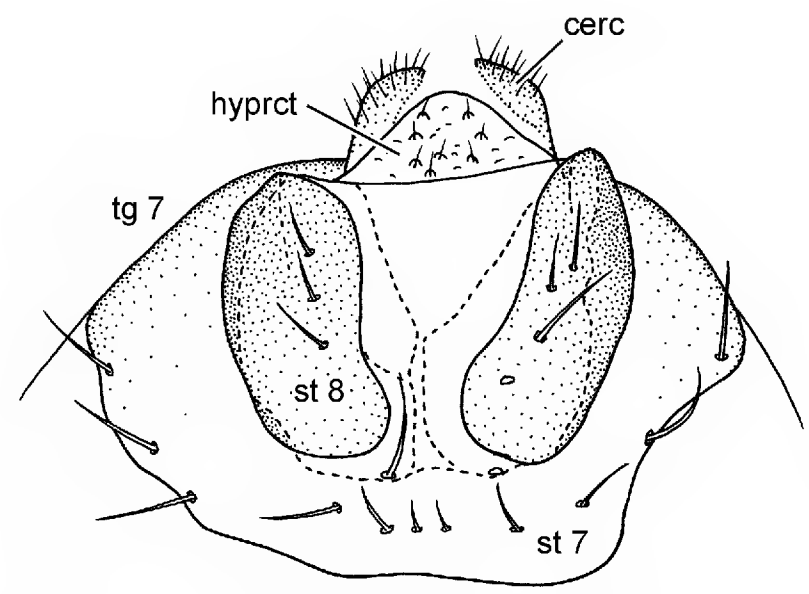
No detailed studies have been undertaken of the egg (*e.g.*, Fig. 89) or larva of any chyromyid species. The little that is known is based on two species of *Chyromya* and one species each in the genera *Aphaniosoma* and *Gymnochiromyia* (all from the western Palaearctic). Some larval characteristics can be deduced from the third-instar and puparium. The cephaloskeleton of *Aphaniosoma* (Fig. 91) was illustrated by Ebejer & Deeming (1997), of *Chyromya* (Fig. 93) by Gibbs (2007) and Rotheray (2011); and of *Gymnochiromyia* (Fig. 92) by Deeming



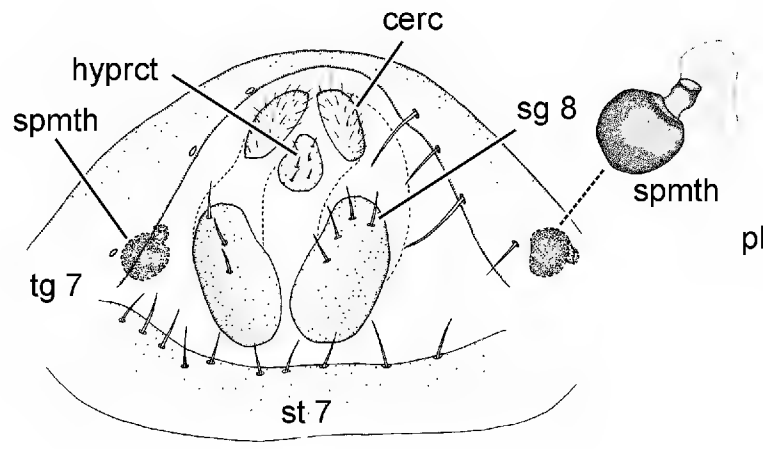
53 *Notiochyromya* ♀



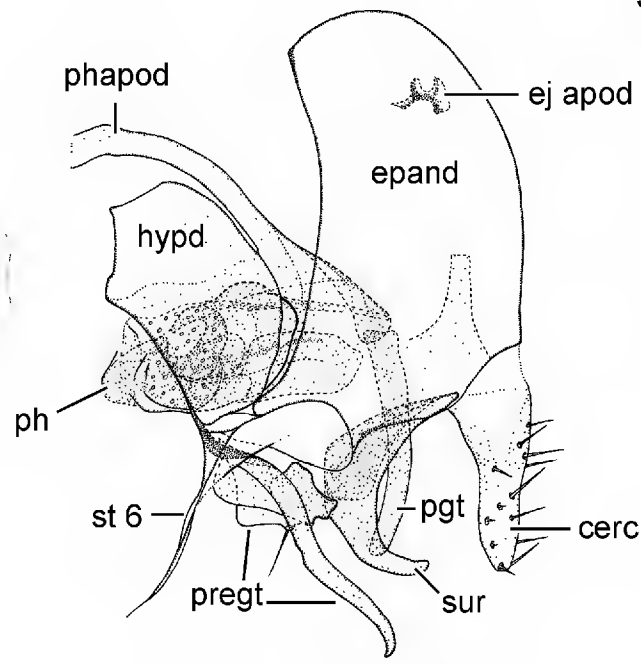
54 *Notiochyromya* ♀



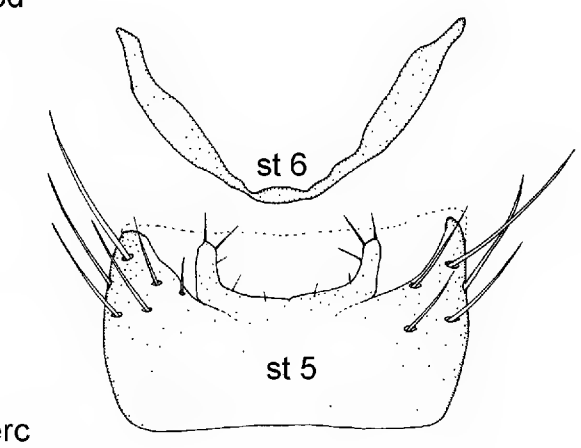
55 *Notiochyromya* ♀



56 *Notiochyromya* ♀



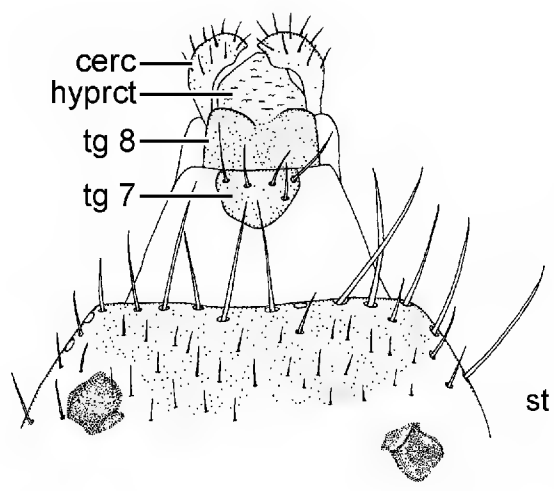
57 *Oroschyromya* ♂



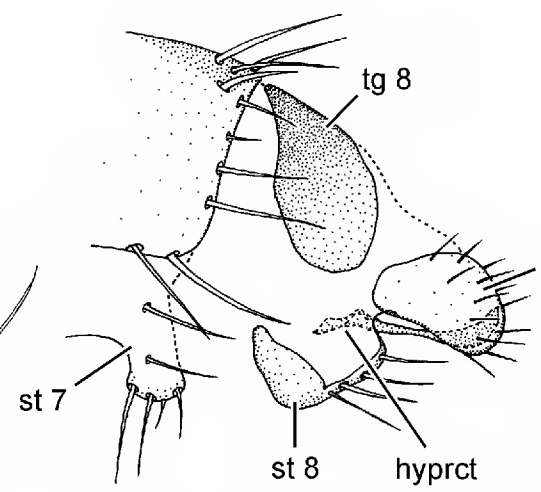
58 *Oroschyromya* ♂

Figs 97.53–58. Male and female terminalia of Chyromyidae: (53) female terminalia of *Notiochyromya* sp. (undescribed species B *sensu* Ebejer 2009), lateral view; (54) same, spermatheca; (55) same, female terminalia, ventral view; (56) same, *N. sexspinosa* (Lamb); (57) male terminalia of *Oroschyromya elongata* Ebejer, lateral view; (58) same, male pregenital sternites, ventral view. Figs 56–58 (Ebejer 2009, figs 10a, 19a, b).

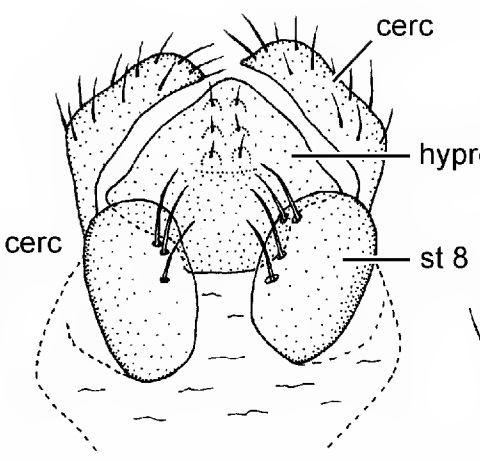
Abbreviations: cerc – cercus; ej apod – ejaculatory apodeme; epand – epandrium; hypd – hypandrium; hyprct – hypoproct; pgt – postgonite; ph – phallus; phapod – phallapodeme; pregt – pregonite; sg – segment; spmth – spermatheca; st – sternite; sur – surstylus; tg – tergite.



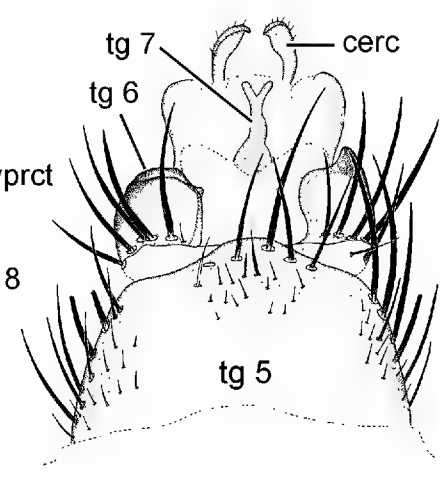
59 *Oroschyromya* ♀



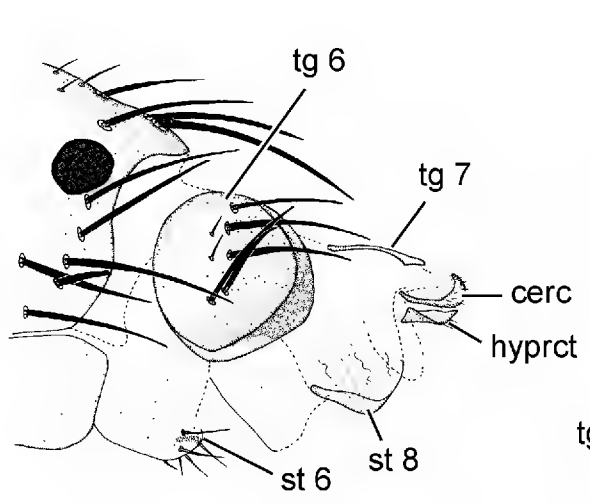
60 *Oroschyromya* ♀



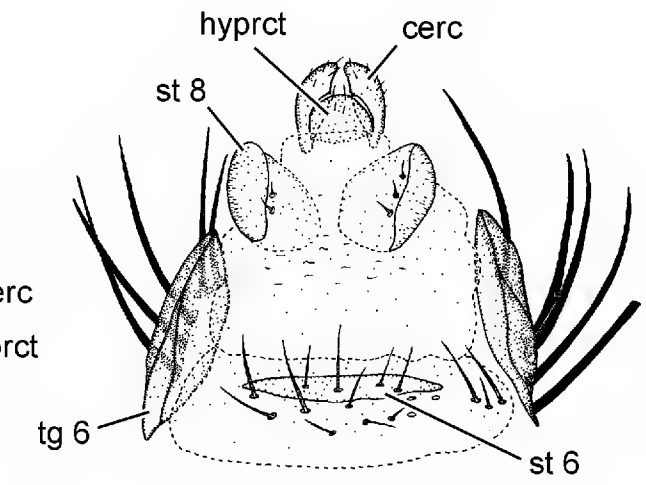
61 *Oroschyromya* ♀



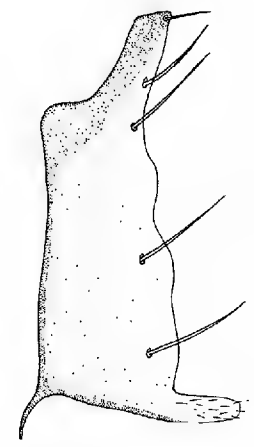
62 *Oroschyromya* ♀



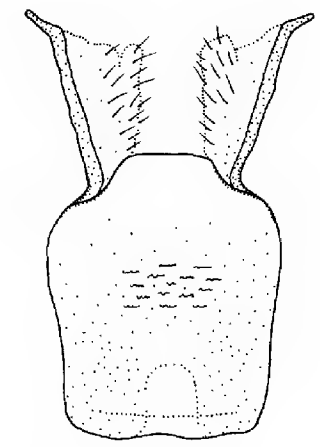
63 *Oroschyromya* ♀



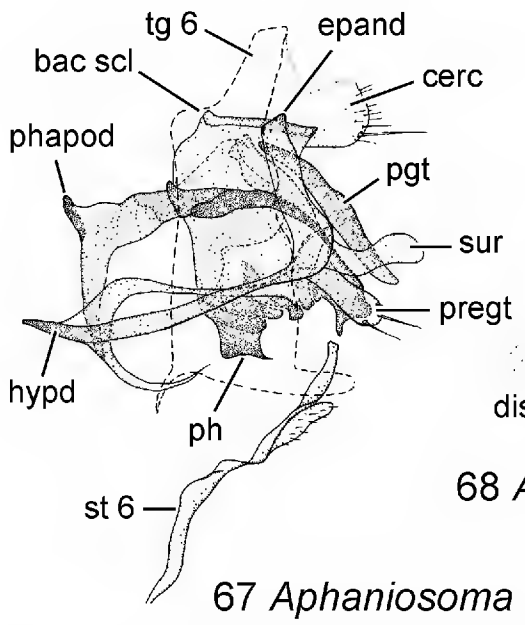
64 *Oroschyromya* ♀



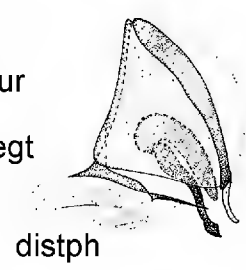
65 *Aphaniosoma* ♂



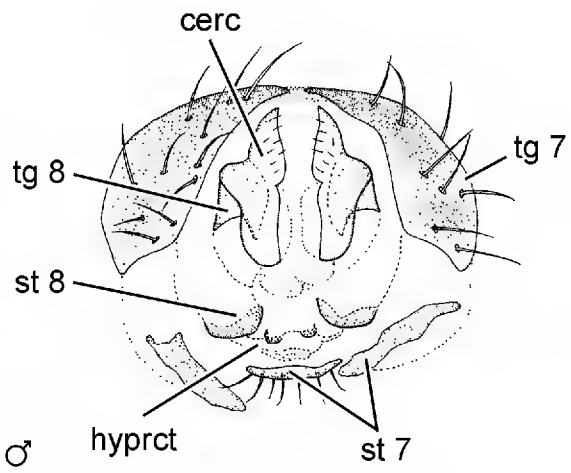
66 *Aphaniosoma* ♂



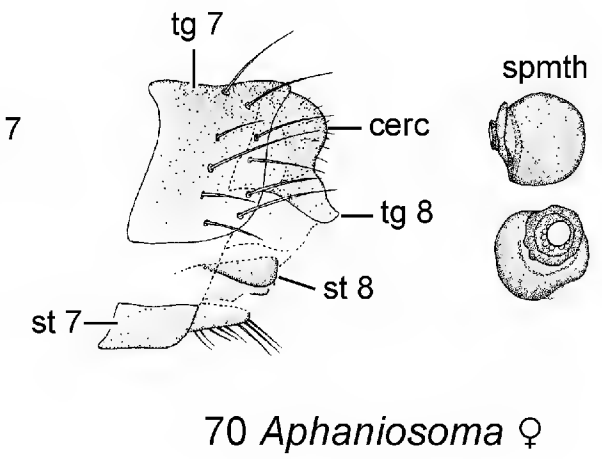
67 *Aphaniosoma* ♂



68 *Aphaniosoma* ♂



69 *Aphaniosoma* ♀



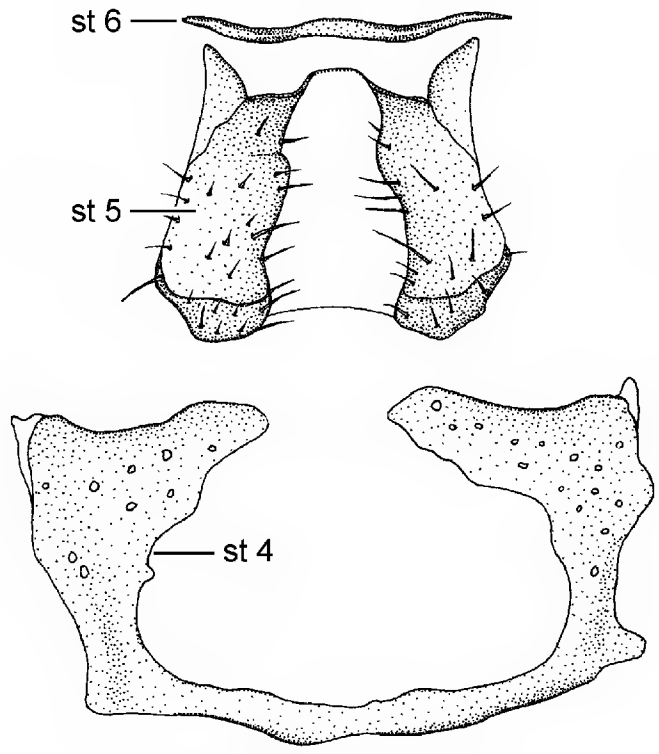
70 *Aphaniosoma* ♀

Figs 97.59–70. Male and female terminalia of Chyromyidae: (59) female terminalia of *Oroschyromya elongata* Ebejer, dorsal view; (60) same, lateral view; (61) same, ventral view; (62) female terminalia of *O. affinis* Ebejer, dorsal view; (63) same, lateral view; (64) same, ventral view; (65) male tergite 6 of *Aphaniosoma fissum* Collin, lateral view; (66) same, male sternite 6, ventral view; (67) same, male terminalia, lateral view; (68) same, detail of distiphallus; (69) same, female terminalia, posterior view; (70) same, lateral view with spermatheca, lateral view (above) posterior view (below). Figs 59–70 (Ebejer 2009, figs 20c, a, b, 13c, b, a, 39a, b, c, 40a, b, c, respectively).

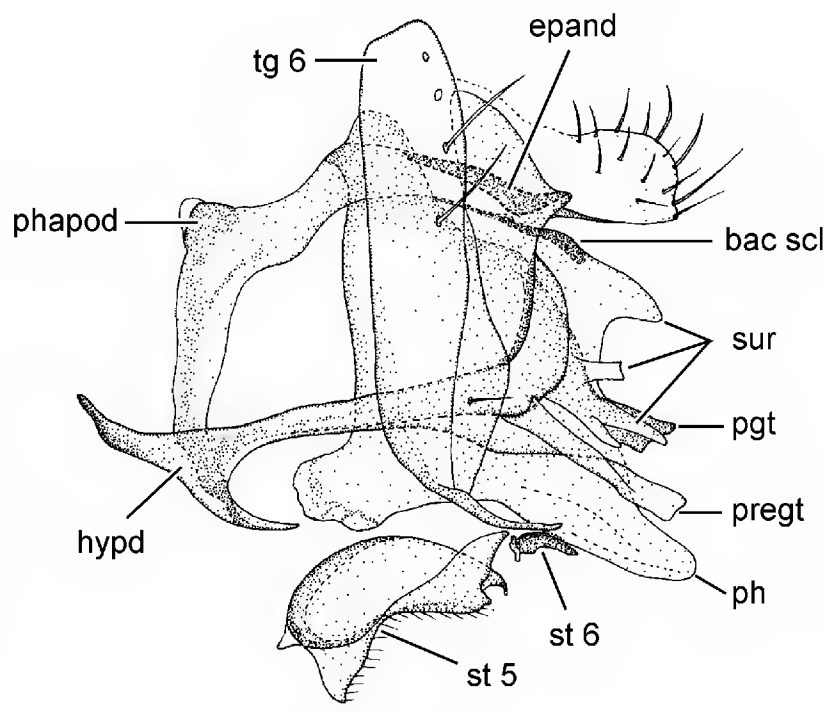
Abbreviations: bac scl – bacilliform sclerite; cerc – cercus; distph – distiphallus; epand – epandrium; hypd – hypandrium; hyprct – hypoproct; pgt – postgonite; ph – phallus; phapod – phallapodeme; pregt – pregonite; spmth – spermatheca; st – sternite; sur – surstylus; tg – tergite.

(1998). The cephaloskeleton has long, curved mouthhooks, that are broad basally and where they articulate ventrally with the small dental sclerite. The mouthhooks are blunt in *Chyromya* and *Gymnochiromyia* and are sharp in *Aphaniosoma*. The caudal end of the mouthhooks articulate with the long, stout, intermediate sclerite, dorsal to which lies a narrow parastomal bar in *Chyromya* and *Gymnochiromyia*, but not in *Aphaniosoma*. The dorsal cornu of the basal sclerite projects caudally into a long narrow pointed dorsal wing and the ventral cornu broadens markedly in *Gymnochiromyia*, but narrows in *Aphaniosoma* and *Chyromya*. The spinules of the ventral creeping welts are sparse in *Gymnochiromyia*, but more numerous in *Aphaniosoma*. The dorsal bridge of the basal sclerite is apparently without a cuticular sieve.

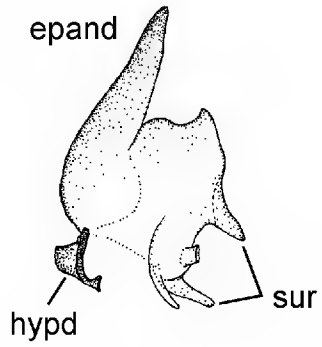
Deeming (1998) described the puparium of *G. inermis*; Ebejer & Deeming (1997) that of *Aphaniosoma zaharensis* Ebejer & Deeming, 1997; and Gibbs (2007) and Rotheray (2011) that of *Chyromya britannica* Gibbs, 2007 and *C. femorellum* (Fallén, 1820). The ground colour of puparia is pale yellow to light brown, with relatively thin integument. The prothoracic spiracles are small and situated on the anterior margin of the prothorax, comprising an inconspicuous fan of 3 papillae. The posterior spiracles are located on a pair of short papillae,



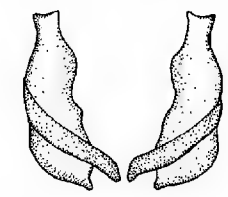
71 *Aphaniosoma* ♂



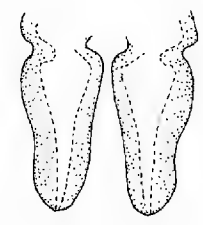
72 *Aphaniosoma* ♂



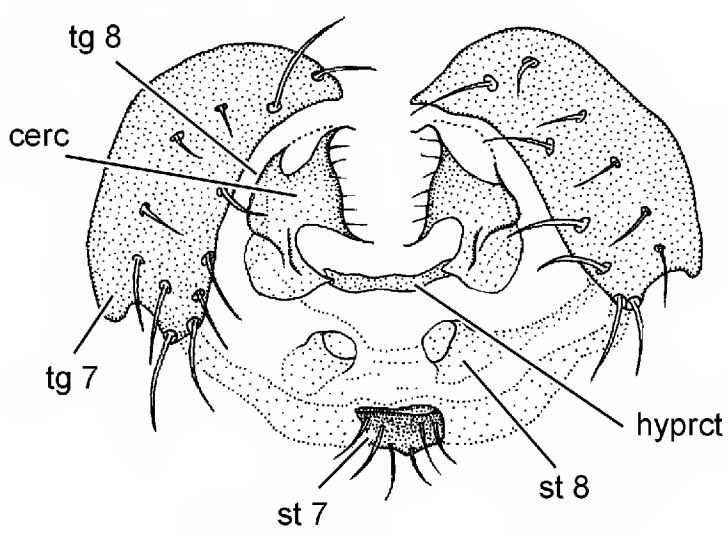
73 *Aphaniosoma* ♂



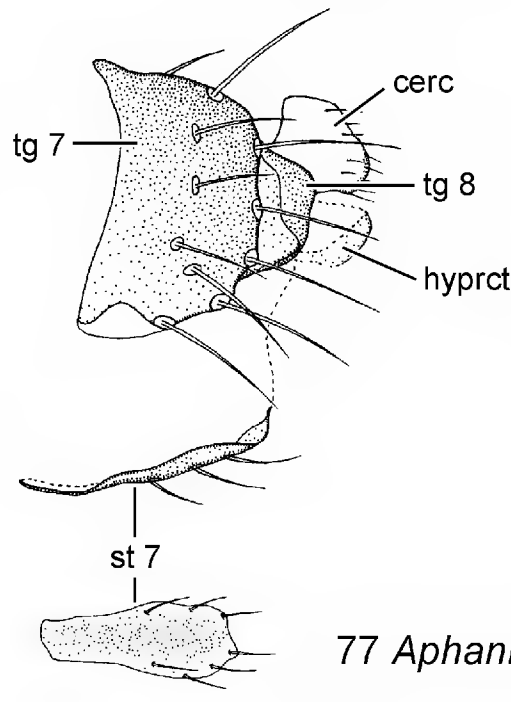
74 *Aphaniosoma* ♂

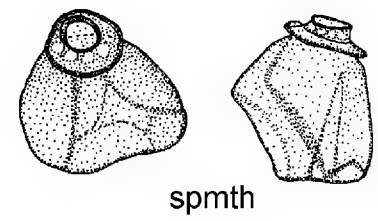


75 *Aphaniosoma* ♂



76 *Aphaniosoma* ♀





77 *Aphaniosoma* ♀

Figs 97.71–77. Male and female terminalia of Chyromyidae: (71) male pregenital sternites of *Aphaniosoma pullum* Ebejer, ventral view; (72) same, male terminalia, lateral view; (73) same, left epandrium posterior view; (74) same, postgonites posterior view; (75) same, distiphallus, ventral view; (76) same, female terminalia, posterior view; (77) same, lateral view (inset right: spermatheca in two views). Figs 71–77 (Ebejer 2009, Figs 50e, a, b, c, d, 51a, b, c, d, respectively).

Abbreviations: bac scl – bacilliform sclerite; cerc – cercus; epand – epandrium; hypd – hypandrium; hyprct – hypoproct; pgt – postgonite; ph – phallus; phapod – phallapodeme; pregt – pregonite; spmth – spermatheca; st – sternite; sur – surstylus; tg – tergite.

which in *Aphaniosoma* arise directly from the puparial surface and are widely separated (Fig. 90), but in *Chyromya* and *Gymnochiromyia* each spiracle is situated on a small papilla, both papillae being closely approximated on a tubercle or ridge, formed by the very narrowed anal compartment. The posterior spiracular plates (e.g., Fig. 90) are minute, with 3 slit-like spiracular openings and a round ecdysial scar and four groups of peristigmatic tufts, each with four short branches.

Economic significance

The Chyromyidae have no known economic importance. There are no records involving any species in agricultural, medical, veterinary or forensic works.

Classification

There are over 189 described species in nine genera globally, two genera of which are currently endemic to the Afrotropical Region. Interpretations of the systematic position of the Chyromyidae has changed over time. Hendel (1916, 1922) grouped the Chyromyidae with the Anthomyzidae and Opomyzidae, adding Clusiidae later. Hennig (1958) could not find a sister-group to the Chyromyidae within the Heleomyzidae, but considered the Chyromyidae as sharing several synapomorphic characters with Aulacigastridae, Anthomyzidae and Opomyzidae. McAlpine (1985) included the following families in the Heleomyzidae: Borboropsidae, Chiropteromyzidae, Cnemospathidae, Heteromyzidae, Notomyzidae, Rhinotoridae (all non-Afrotropical) and Trixoscelididae, but excluded Chyromyidae and Sphaeroceridae, although he accepted that these two families were closely related to the Heleomyzidae, as did McAlpine (1987). Later, McAlpine (1989) placed all these families, including the Chyromyidae in the Sphaeroceroidea. Most recently, McAlpine (2007) argued that the Sphaeroceridae and Heleomyzidae should be classified together in a single family, the Heteromyzidae. He excluded the Chyromyidae on the grounds that there remain several distinct morphological characters too far removed from his proposed ground-plan of his concept of the Heteromyzidae. Ebejer (2009) accepted this view. Some other authors, however, have not (Marshall *et al*. 2011). Wiegmann *et al*. (2011) utilising molecular techniques were unable to resolve the phylogenetic relationships of many acalyptrate families, including the Chyromyidae. There is still no convincing evidence available to support or refute the above considerations. Ebejer (2009) gave a cladistic analysis based on morphology of the Chyromyidae, which he divided into two subfamilies: Chyromyinae and Aphaniosominae.

Identification

The main characters used to distinguish chyromyids are: small size; head with distinct medial and lateral vertical setae; postocellar setae (or setulae) if present, parallel or convergent; wing with costagial break at junction with R_1; vein R_{2+3} symmetrically arcuate, gradually converging towards vein R_{4+5} apically; discal, basal and anal cells always present; absent pre-apical tibial seta.

The non-Afrotropical genus *Chyromya* is included in the below identification key, in the event that the genus is later recorded from the region. The genus is not included in the "Synopsis of the fauna" section below. Chyromyidae are normally either point-mounted, micro-pinned in the field for later double-mounting or are preserved in ethanol (see Chapter 2).

Key to genera of Afrotropical Chyromyidae

1. Head with occiput convex to flat, never distinctly concave, with 3 well-developed fronto-orbital setae, anterior usually inclinate (e.g., Figs 2–5); scutum without intra-postpronotal setae (e.g., Figs 34–37); wing veins R_{4+5} and M_1 parallel or slightly convergent towards apex (e.g., Figs 18–21); mid tibia without apicoventral seta, if seta present (some *Notiochyromya* and *Somatiosoma*), then not longer than diameter of tibia at apex (e.g., Figs 26, 27, 31); scutellum often with additional marginal or discal setulae and/or setae (e.g., Figs 35, 37); male postabdomen with more or less hemispherical epandrium, entirely external to tergite 6 (e.g., Figs 44, 45, 50, 57) (CHYROMYINAE) 2

– Head with occiput concave, with 0–6 fronto-orbital setae of variable length, never inclinate, if more than 2, these usually short and progressively shorter anteriorly (e.g., Figs 6–9); scutum with inclinate intra-postpronotal seta or setula (except in *Krifomyia* and *Tethysimyia*) (e.g., Figs 38, 40); wing veins R_{4+5} and M_1 parallel (*Krifomyia* and *Paraphaniosoma*) (e.g., Figs 23, 24), convergent (*Tethysimyia*) (e.g., Fig. 25) or divergent (*Aphaniosoma*) (e.g., Fig. 22) towards apex; mid tibia invariably with long apicoventral seta (e.g., Figs 28, 29, 32, 33); scutellum never with more than 2 pairs of marginal setae (e.g., Figs 38–41); male postabdomen never with hemispherical epandrium, this partially or entirely enclosed within tergite 6 (e.g., Figs 67, 72, 78, 82, 84) (APHANIOSOMINAE). 6

2. Thorax with distinct prealar seta, posterior to transverse suture in depression between notopleuron and scutum (Figs 35, 43); presutural dorsocentral setae absent; acrostichal setae never differentiated from numerous scutal setulae, except 2–4 prescutellar acrostichal setae (Fig. 35); head in profile (Fig. 3) with longest part towards lower eye margin; gena (Fig. 3) narrow, < ½ height of eye at middle; mid tibia sometimes with short apicoventral seta (shorter than diameter of tibia at apex) . . . . . *Notiochyromya* Ebejer

– Thorax without distinct prealar seta (e.g., Figs 34, 36, 37), if setulae present in this area, then these similar to setulae elsewhere on scutum; if setula in this position interpreted as a short prealar seta (some

non-Afrotropical *Chyromya* and *Gymnochiromyia*), then mid tibial apicoventral seta entirely absent (e.g., Fig. 26); presutural dorsocentral seta may be present and acrostichal setae often differentiated; head, in profile, longer towards upper eye margin and gena usually broader than ½ height of eye at middle (e.g., Figs 2, 4, 5) 3

3. Scutum with well-developed intrapostalar seta present (Fig. 36); scutellum bare on disc, with only 2 pairs of marginal setae (Fig. 36); frons at eye margins significantly narrower towards antennae (*i*.e., strongly convergent anteriorly) (Fig. 4); male terminalia with cerci distinctly modified or spinose (Fig. 57). . . . . *Oroschyromya* Ebejer

– Scutum without intra-postalar seta, if seta or setula present, then these shorter than prescutellar acrostichal setae (e.g., Figs 34, 37); scutellum with or without additional marginal or discal setae; frons at eye margins usually less markedly convergent (e.g., Figs 2, 5); male terminalia with cerci simple (e.g., Figs 44, 45, 50). 4

4. Head with occiput distinctly convex, with numerous setae and setulae on disc in addition to those around occipital foramen and on postocular margin; frons parallel-sided or virtually so; discal medial wing cell (*dm*) usually extending beyond middle of wing; male with dilated femora (non-Afrotropical) . . . . . [*Chyromya* Robineau-Desvoidy]

– Head with occiput flat or slightly concave, without occipital setulae on disc, although rarely 2 or 3 short setulae may be present outside postocular row on each side; frons with sides converging towards antennae (e.g., Figs 2, 5); discal medial wing cell (*dm*) extends only to middle of wing (e.g., Figs 18, 21); male with little or no femoral dilation. 5

5. Scutellum disc bare, with usual 2 pairs of marginal setae (Fig. 34); presutural dorsocentral sometimes present; prescutellar acrostichal setae longer than any setulae that may be situated in intrapostalar area; never with strong apicoventral seta on mid tibia (Fig. 26) . . . . . .*Gymnochiromyia* Hendel

– Scutellum with setulae on disc (Fig. 37), sometimes with an additional marginal seta as well as usual 2 pairs; presutural dorsocentral seta absent (Fig. 37); prescutellar acrostichal setae or setulae poorly developed; short mid tibial apicoventral seta often present (Fig. 31). . . . . .*Somatiosoma* Frey

6. Thorax with scutal setulae in 2 acrostichal rows (Fig. 38), sometimes irregular; medially directed intra-postpronotal seta/setula almost always present; supra-alar and intrapostalar setae absent (Fig. 38); wing veins R_{4+5} and M_1 always divergent towards wing apex (Fig. 22) . . . . . .*Aphaniosoma* Becker

– Thorax with scutal setulae in 4–10 rows, not differentiated into acrostichal setae (e.g., Figs 39–41); medially directed intra-postpronotal seta/setula sometimes present (e.g., Fig. 40); at least intrapostalar seta present, even if short (e.g., Figs 39–41); wing veins R_{4+5} and M_1 parallel or convergent towards wing apex (e.g., Figs 23–25) 7

7. Thorax with prealar seta in depression posterior to scutal transverse suture (Fig. 40); medially directed intra-postpronotal setula present; supra-alar setula distinct (Fig. 40); wing veins R_{4+5} and M_1 parallel (Fig. 24); head longer than high (Fig. 8); eye margins on frons strongly convergent towards antennae; frons never inflated and not projecting above and anterior to eye margin (Fig. 8); 1–3 well-developed reclinate fronto-orbital setae (Fig. 8); paravertical setae often absent, but if present, usually only 1 minute setula or entirely missing in some specimens (Fig. 8); facial carina very indistinct, at most just discernible immediately below lunule only; gena narrow, less than ½ height of eye (Fig. 8) . . . . . .*Paraphaniosoma* Ebejer

– Thorax without prealar and supra-alar setae, if supra-alar present, not easily differentiated from adjacent setulae; intra-postpronotal setulae absent (e.g., Figs 39, 41); wing veins R_{4+5} and M_1 parallel or convergent towards wing apex (e.g., Figs 23, 25); head higher than long; frons parallel-sided or virtually so, projecting anteriorly above antennae, appearing somewhat inflated (e.g., Figs 7, 9); 0–4 short and usually inconspicuous fronto-orbital setae (e.g., Figs 7, 9); paravertical setae present or absent (e.g., Figs 7, 9), if present, invariably very short; facial carina distinct; gena broad, often conspicuously broader than ½ height of eye (e.g., Figs 7, 9). 8

8. Head with facial carina exceptionally well-developed, broadening below antennae (Fig. 7); antennae inserted in deep fossae; gena very broad, almost equal to height of eye or more (Fig. 7); thorax without katepisternal seta; scutal setulae in 4–6 irregular rows between dorsocentral lines, short and sparse (Fig. 39); other scutal setulae sparse, short to minute; wing veins R_{4+5} and M_1 parallel to apex of wing; humeral crossvein (*h*) thickened (Fig. 23) . . . . . *Krifomyia* Ebejer

– Head with facial carina narrow, less conspicuous and widened below antennae (Fig. 9); antennae, although appearing recessed, not inserted in deep fossae; gena approximately as broad as ½ height of eye, or slightly more (Fig. 9); thorax with katepisternal seta (as in Figs 42, 43); acrostichal setulae in 4–10 rows, more numerous and longer, other scutal setulae more numerous and longer; wing veins R_{4+5} and M_1 convergent towards apex of wing; humeral crossvein (*h*) unmodified (Fig. 25) . . . . . *Tethysimyia* Ebejer

Synopsis of the fauna

Although Chyromyidae from several sub-Saharan countries have been studied, most material originates from South Africa and Namibia, with the Brandberg massif in the latter country receiving special attention (Ebejer 2000). The Arabian Peninsula has also been relatively well-studied (Ebejer 1996, 2008*b*).

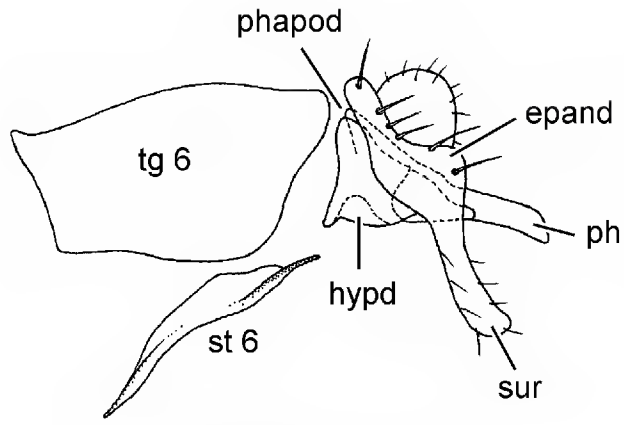
***Aphaniosoma* Becker** (Aphaniosominae)**.** A genus of 126 described species, occurring in the Afrotropical, Nearctic and Palaearctic Regions, with 30 species recorded from the Afrotropics, although many more can be expected. The genus is widespread in the continental Afrotropics and on oceanic islands. It is easily recognised by the following combination of characters: occiput concave; acrostichal setae in 2 rows and propleural setula present; costal vein (C) broken slightly beyond humeral crossvein and at apex of vein R_1; veins R_{4+5} and M_1 divergent towards wing apex (Fig. 22); and with a strong apicoventral seta on mid tibia invariably present, that is longer than the diameter of the tibia at its apex (Fig. 28). The male terminalia are illustrated in Figs 65–68 and 71–75 and the female terminalia in Figs 69, 70, 76 and 77. *Aphaniosoma* has a predilection for hot and dry habitats. The majority of species have a strong affinity to dunes and the shores of standing water bodies, particularly saline marshes. In localities with saline marshes, flies exhibit a strong association with certain plants, including *Tamarix* (Tamaricaceae), Chenopodiaceae and *Phragmites* and other Poaceae. An identification key to Afrotropical species was provided by Ebejer (2009).

***Gymnochiromyia* Hendel** (Chyromyinae)**.** A genus of 31 described species occurring in the Afrotropical, Nearctic and Palaearctic Regions, with 16 species in the Afrotropics. Most Afrotropical species occur in Southern Africa and more are likely to be discovered. Species of the genus are relatively uniform in appearance and identification can be problematic. *Gymnochiromyia* lack setulae or setae on the scutellum (other than the usual basal and subapical marginal pairs) and are also recognisable by the absence of prealar and intrapostalar setae (Fig. 34); the oval eyes lie horizontally or obliquely (Fig. 2); the frons protrudes above the antennae, so is visible in profile to a greater or lesser extent (Fig. 2); and the apicoventral seta on the mid tibia is absent (Fig. 26). The male terminalia are illustrated in Fig. 50 and the female terminalia in Figs 51 and 52. The habitus of most species appears more slender and less setulose than *Notiochyromya* and *Oroschyromya*, with which genera *Gymnochiromyia* may be confused. Most species occur on vegetated dunes in drier and warmer areas within a generally temperate climate. In Europe, several species have an affinity for open oak woodland (Ebejer 2010). Ebejer (2008*a*) reviewed the Afrotropical species of this genus and provided an identification key.

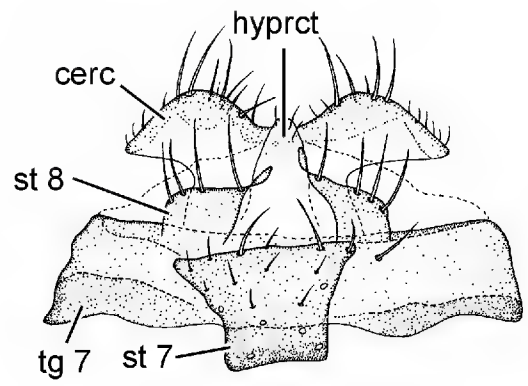
***Krifomyia* Ebejer** (Aphaniosominae)**.** An endemic monotypic genus with the single species, *K. minutissima* (Bezzi, 1908), known only from the coast of Namibia. Two undescribed Neotropical species may eventually belong here. A few more species might be expected. It is characterised by the rather square, short head and the inflated frons, that has parallel margins and which, in profile, is visible all along the eye margin from the vertex to the antenna (Fig. 7). It has a well-developed, broad facial carina extending from the lunule to just below the antennae, where it broadens above the oral margin, leaving the antennae in deep pits (Fig. 7). The intra-postpronotal, presutural, supra-alar and katepisternal setae are absent (Fig. 39); wing veins R_{4+5} and M_1 converge slightly towards the apex (Fig. 23) and an apicoventral seta is present on the mid tibia (Fig. 32). The male terminalia are illustrated in Figs 78 and 79 and the female terminalia in Figs 80 and 81. *Krifomyia* is a rare and cryptic inhabitant of hot and dry coastal regions. The described species can be identified using Ebejer (2009).

***Notiochyromya* Ebejer** (Chyromyinae)**.** A genus of eight described species occurring in the Afrotropical, Australasian, Neotropical and Oriental Regions, with five species in the Afrotropics. Several undescribed species, 6–7 extralimital and three from Southern Africa (not described due to insufficient material), are known to the writer. More Afrotropical species are likely to be discovered. The genus is recognised by the following combination of characters: the frons measured at the level of the anterior ocellus is narrower than $^1/_3$ the width of head, with margins strongly convergent towards lunule; the frons in profile is inclined more towards the vertical than the horizontal, thus the maximum length of the head when viewed in profile is closer to lower eye margin than upper (Fig. 3); the occiput is concave, a prealar seta is present, the posterior intra-alar and presutural dorsocentral setae are absent (Fig. 35). The scutellum usually exhibits additional marginal or discal setae (not setulae), or both (Fig. 35). A short apicoventral seta is usually present on the mid tibia. In general appearance, species in this genus present a head narrower than the thorax and an epandrium that is relatively small in comparison to the remainder of the abdomen (similar to *Somatiosoma*, but in contrast to *Gymnochiromyia* and *Oroschyromya*). The robust thorax is densely clothed in fine setulae over the entire scutum (Fig. 35). Strong prescutellar acrostichal setae are present, often four setae in one transverse row; dorsocentral, intrapostalar and postalar setae are set well back and usually brown or black (Fig. 35). The abdomen frequently has matt or shiny brown or black maculae or fasciae on tergites (Figs 48, 49). The female terminalia are illustrated in Figs 53–56. Species of *Notiochyromya* prefer hot and wet (at least seasonally) environments. Most species inhabit forests or forest margins, including those encroaching on the sea shore. *Notiochyromya sexspinosa* (Lamb, 1914) has been collected from cave entrances in Nigeria (J.C. Deeming, pers. comm. 2012). An identification key to Afrotropical species was provided by Ebejer (2009).

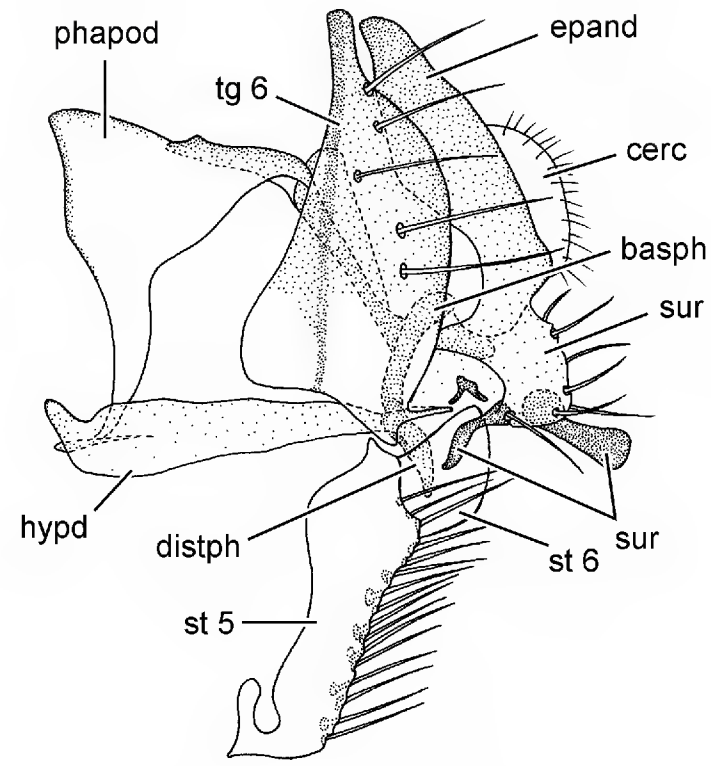
***Oroschyromya* Ebejer** (Chyromyinae)**.** A genus of nine described species occurring in the Afrotropical and Oriental Regions, with eight species on the Afrotropics. *Oroschyromya* is distinguished by having the head broader than the thorax; the frons narrow, with moderate to strongly converging margins; the eye oval, lying oblique in profile (Fig. 4); there is a well-developed intrapostalar seta; the scutellum has no additional marginal setae or setulae on the disc (Fig. 36); the apicoventral seta on the mid tibia is short or absent (Fig. 27); the male terminalia (Figs 57, 58) have the epandrium large, more or less rectangular in shape and positioned vertically relative to the long axis of the abdomen (*i*.e., in profile higher than long); the male cercus is modified and the pregonites heavily sclerotised, conical to pyramidal in shape. The male terminalia are illustrated in Figs 57 and 58 and the female terminalia in Figs 59–64. Species in this genus favour tropical, montane, well-vegetated



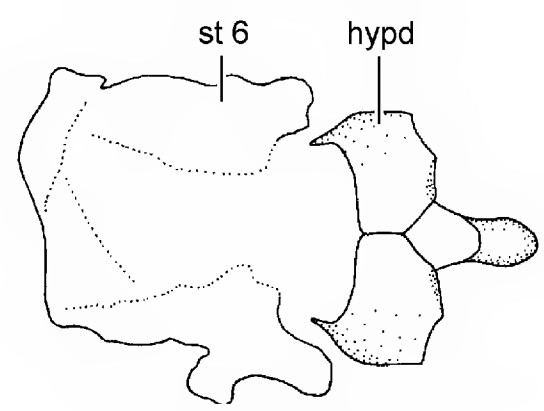
78 *Krifomyia* ♂



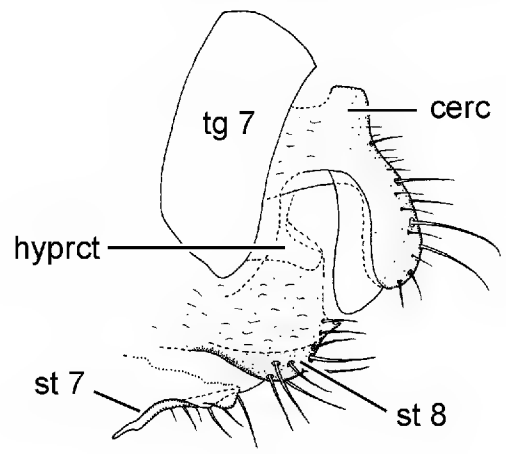
80 *Krifomyia* ♀



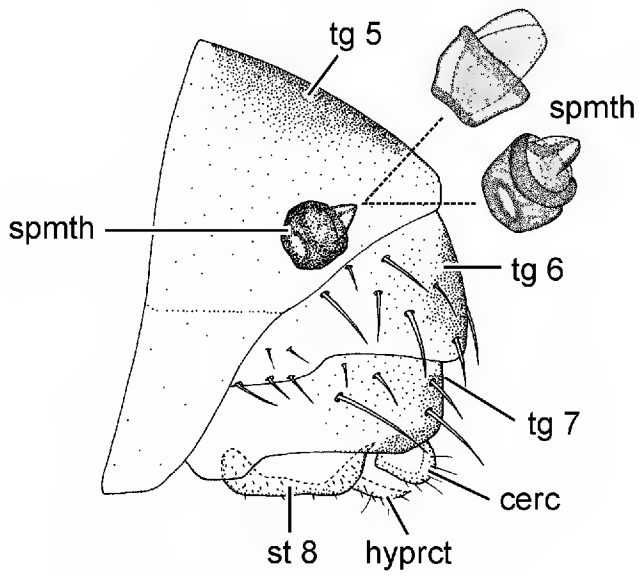
82 *Paraphaniosoma* ♂



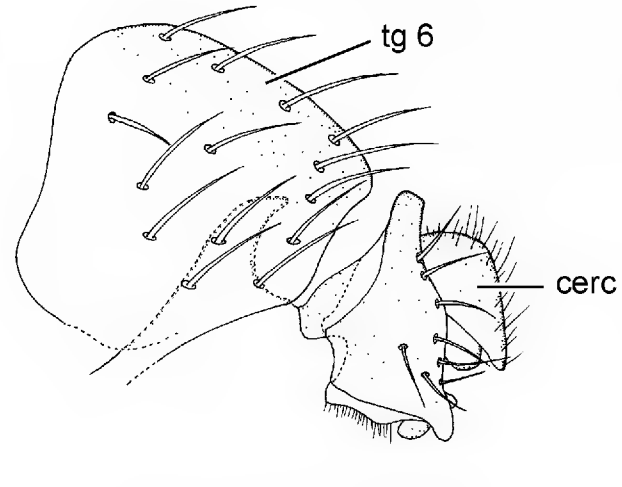
79 *Krifomyia* ♂



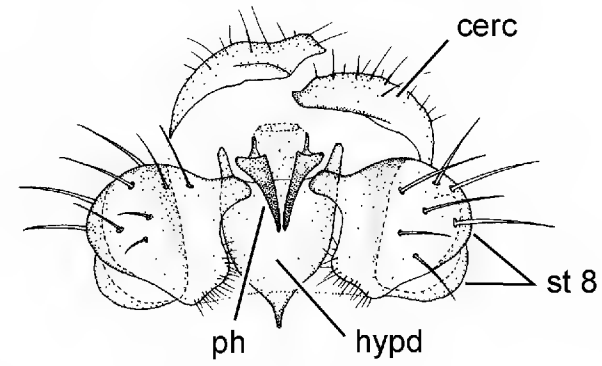
81 *Krifomyia* ♀



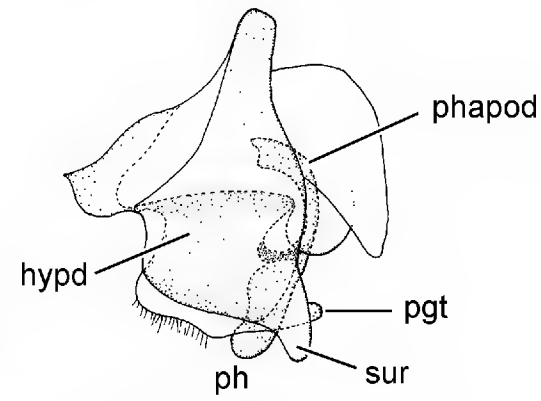
83 *Paraphaniosoma* ♀



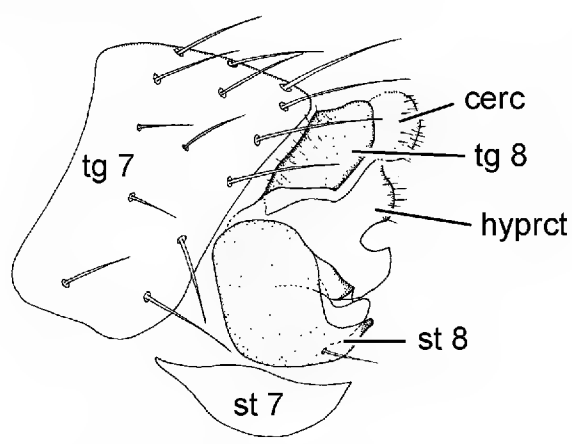
84 *Tethysimyia* ♂



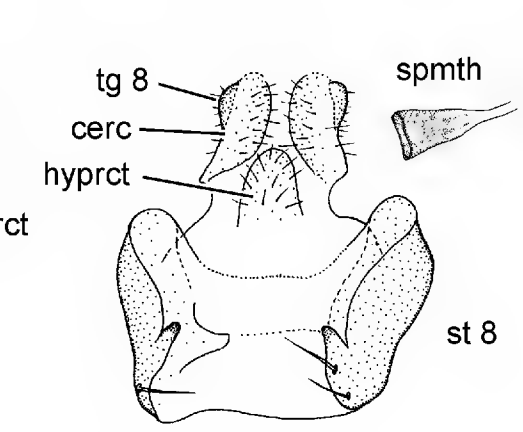
85 *Tethysimyia* ♂



86 *Tethysimyia* ♂



87 *Tethysimyia* ♀



88 *Tethysimyia* ♀

Figs 97.78–88. Male and female terminalia of Chyromyidae: (78) male terminalia of *Krifomyia minutissima* (Bezzi), lateral view; (79) same, ventral view; (80) same, female terminalia, ventral view; (81) same, lateral view; (82) male terminalia of *Paraphaniosoma sexvittatum* (Lamb), lateral view; (83) same, female terminalia; (84) male terminalia of *Tethysimyia deemingi* (Ebejer), lateral view; (85) same, posteroventral view; (86) same, male phallic complex, lateral view; (87) same, female terminalia, lateral view; (88) same, ventral view. Figs 78–88 (Ebejer 2009, figs 56c, d, 57a, b, 58a, 59a, 60a, b, c, 61a, b).

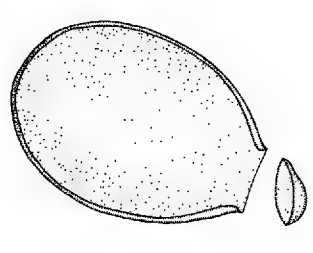
Abbreviations: basph – basiphallus; cerc – cercus; distph – distiphallus; epand – epandrium; hypd – hypandrium; hyprct – hypoproct; pgt – postgonite; ph – phallus; phapod – phallapodeme; spmth – spermatheca; st – sternite; sur – surstylus; tg – tergite.

habitats with a wide range of rainfall. An identification key to Afrotropical species was provided by Ebejer (2009).

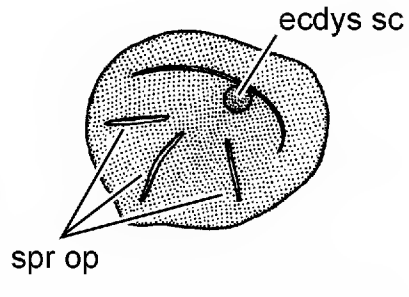
Paraphaniosoma **Ebejer** (Aphaniosominae)**.** A genus of two described species, one from the Oriental Region and one, *P. sexvittatum* (Lamb, 1914), from the Afrotropics. The genus is more widely distributed, however, with nine undescribed extralimital species known from the Australasian, Neotropical and Palaearctic (Far East) Regions. A few more Afrotropical species can be expected. It can be recognised by the well-developed prealar and intrapostalar setae, the acrostichal setae are arranged in six or more rows, only one strong dorsocentral seta present, reduced or absent postvertical setae (Fig. 40) and a strong apicoventral seta on the mid tibia, that is longer than the diameter of the tibia at its apex (Fig. 33). The male terminalia are illustrated in Fig. 82 and the female terminalia in Fig. 83. *Paraphaniosoma* mainly occur in coastal and estuarine localities in hot tropical and subtropical climates. An identification key to Afrotropical species was provided by Ebejer (2009).

Somatiosoma **Frey** (Chyromyinae)**.** A near-endemic genus of seven described species, two of which also extend into the southern Palaearctic Region (Middle East). More species can be expected to be discovered, even outside the Afrotropics. The genus occurs widely in the region, from Cabo Verde in the west, through most countries of continental Africa, to Madagascar and the smaller Indian Ocean islands. *Somatiosoma* is recognised by the absent presutural dorsocentral setae, prealar and intrapostalar setae and additional marginal setae on the scutellum, but with setulae on the scutellar disc (Fig. 37). The male abdomen is illustrated in Fig. 44, the terminalia in Fig. 45 and the female terminalia in Figs 46 and 47. *Somatiosoma* is the most arid-tolerant genus in the family and species are more likely to be found in scrub vegetation in eremic zones. It appears to be the only genus of its subfamily to occur in deserts. An identification key to Afrotropical species was provided by Ebejer (2009).

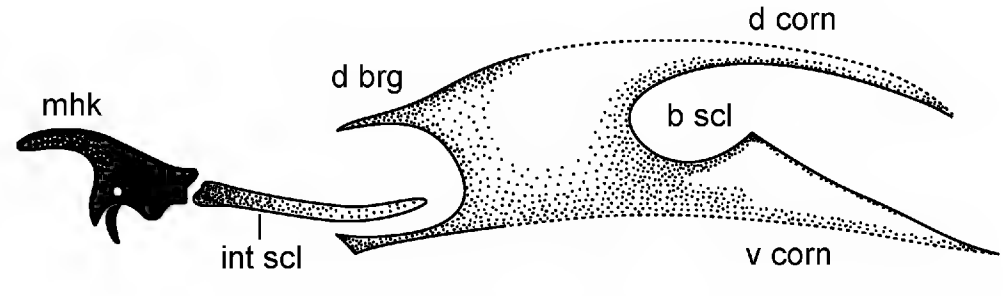
Tethysimyia **Ebejer** (Aphaniosominae)**.** A genus of four described species occurring in the Palaearctic, Neotropical and Oceanian Regions. The single Afrotropical species, *T. deemingi* (Ebejer, 1996), occurs in the Sinai Peninsula of Egypt and Arabian islands in the southern Red Sea. There are undescribed species from various Caribbean islands and more can be expected. *Tethysimyia* are very small pale flies, with a rather large round head or head higher than long; a very broad gena; a well-developed, but narrow facial carina (not reaching the mouth margin); and a recessed antenna, but these not in deep fossae; the vestiture is generally reduced and fine; there are two very short fronto-orbital setae inserted high on the frons (Fig. 9); the scutum has one dorsocentral seta, the acrostichal setae are arranged in 4–10 rows, the prealar and supra-alar setae are absent, but the postalar and sometimes a short intrapostalar seta are present (Fig. 41), as is a short katepisternal seta on the pleura. Wing veins R_{4+5} and M_1 are slightly convergent (Fig. 25). The male postabdomen is exceptionally small, with a dorsally narrow, complete epandrium. The male terminalia are illustrated in Figs 84–86 and the female terminalia in Figs 87 and 88. The genus is associated with saline marshes and mangroves in coastal localities in hot tropical and subtropical climates. An identification key to Afrotropical species was provided by Ebejer (2009).



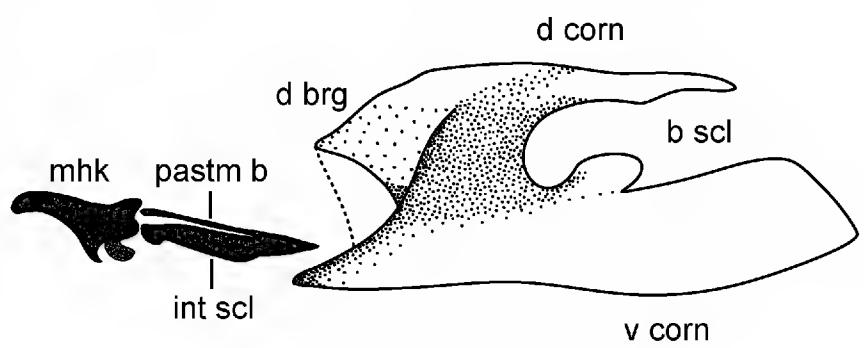
89 *Notiochyromya*



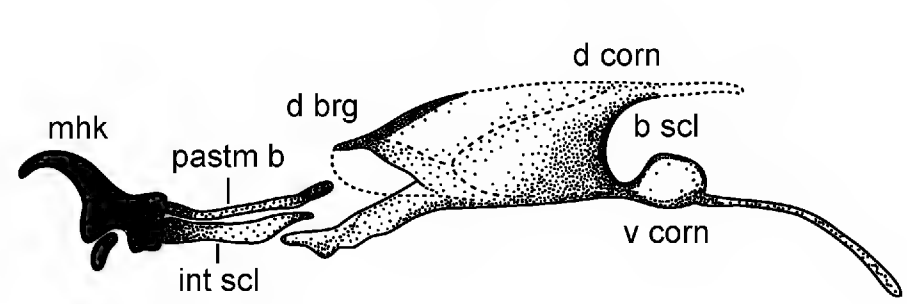
90 *Gymnochiromyia*



91 *Aphaniosoma*



92 *Gymnochiromyia*



93 *Chyromya*

Figs 97.89–93. Immature stages of Chyromyidae: (89) egg of *Notiochyromya sexspinosa* (Lamb), lateral view; (90) posterior spiracular plate of third-instar larva of *Gymnochiromyia inermis* Collin (non-Afrotropical); (91) cephaloskeleton of *Aphaniosoma zaharensis* Ebejer & Deeming, lateral view (non-Afrotropical); (92) same, *G. inermis* (non-Afrotropical); (93) same, *Chyromya britannica* Gibbs (non-Afrotropical). Fig. 89 (Ebejer 2009, fig. 10b), Fig. 90 (after Deeming 1998, fig. 3), Fig. 91 (after Ebejer & Deeming 1997, fig. 6), Fig. 93 (Gibbs 2007, fig. 10).

Abbreviations: b scl – basal sclerite; d brg – dorsal bridge; d corn – dorsal cornu; ecdys sc – ecdysial scar; int scl – intermediate sclerite; mhk – mouthhook; pastm b – parastomal bar; spr op – spiracular openings; v corn – ventral cornu.

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HELEOMYZIDAE 98

(Heleomyzid Flies)

Andrzej J. Woźnica and Ashley H. Kirk-Spriggs

Fig. 98.1. Copulating pair of *Suillia ingens* (Lamb) (Tanzania) (photograph © S.A. Marshall).

Diagnosis

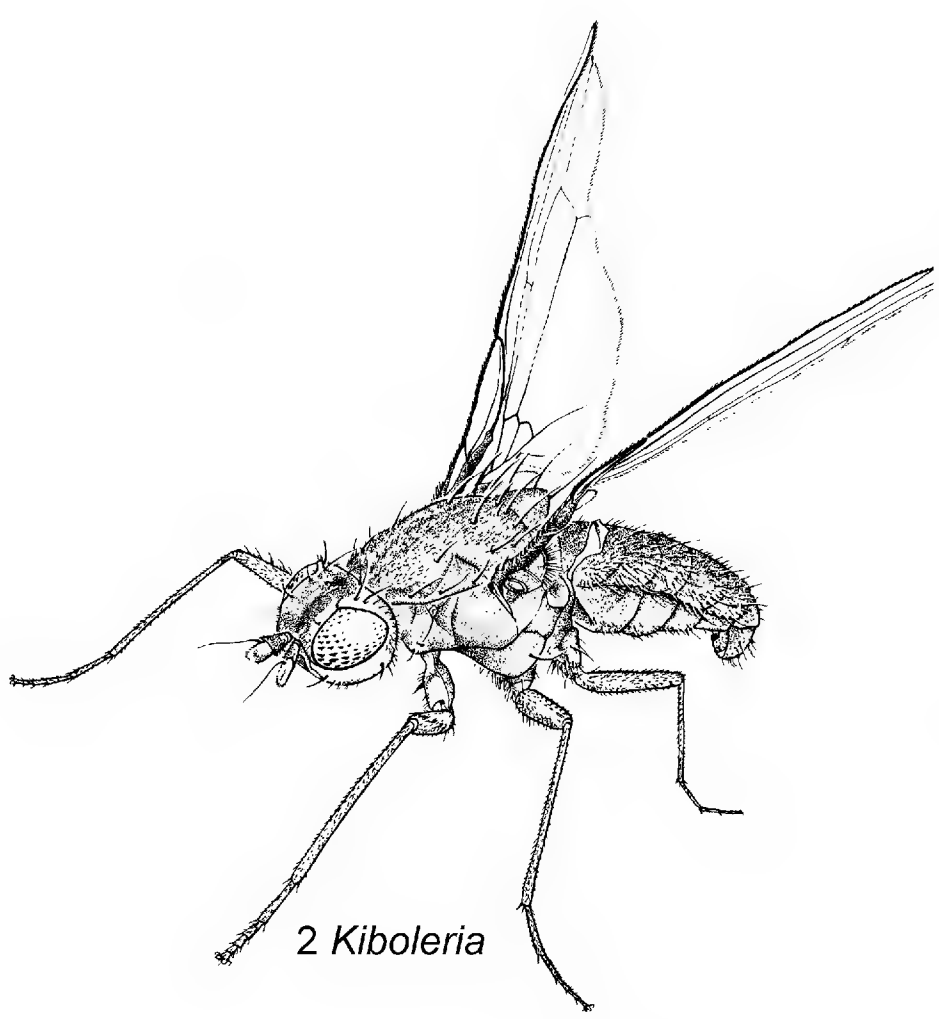
Small- to large-sized (body length: 1.5–13 mm; usually 4–6 mm) acalyptrate flies (Figs 1–5) with yellowish, brownish or blackish body colouration (Fig. 1) and wing membrane hyaline, often with contrasting whitish and dark grey areas, often maculate with crossveins infuscate.

Head (Figs 6–19) with compound eyes widely separated at vertex (all Afrotropical species); medial part of facial plate (postfrons) less sclerotised than lateral parts; frons often with scattered setulae, usually broad, sometimes slightly narrowed anteriorly; orbital plates present (Figs 14–18), usually pruinescent, extending anteriorly from vertical setae; postocellar setae (Figs 14–18) distinctly cruciate; ocellar setae and inner and outer vertical setae strongly developed (Figs 14–18); 1–2 frontoorbital setae present, reclinate or lateroclinate; 1–2 pairs of well-developed vibrissae present, with 1 or more rows of subvibrissal setae and 1 or more strong genal setae; antennal pedicel without dorsal seam; postpedicel without basal process projecting into pedicel, rounded or with slight, blunt apical dorsal angle (in lateral view); arista (Figs 14–19) minutely pubescent to plumose; proboscis and palpus well-developed.

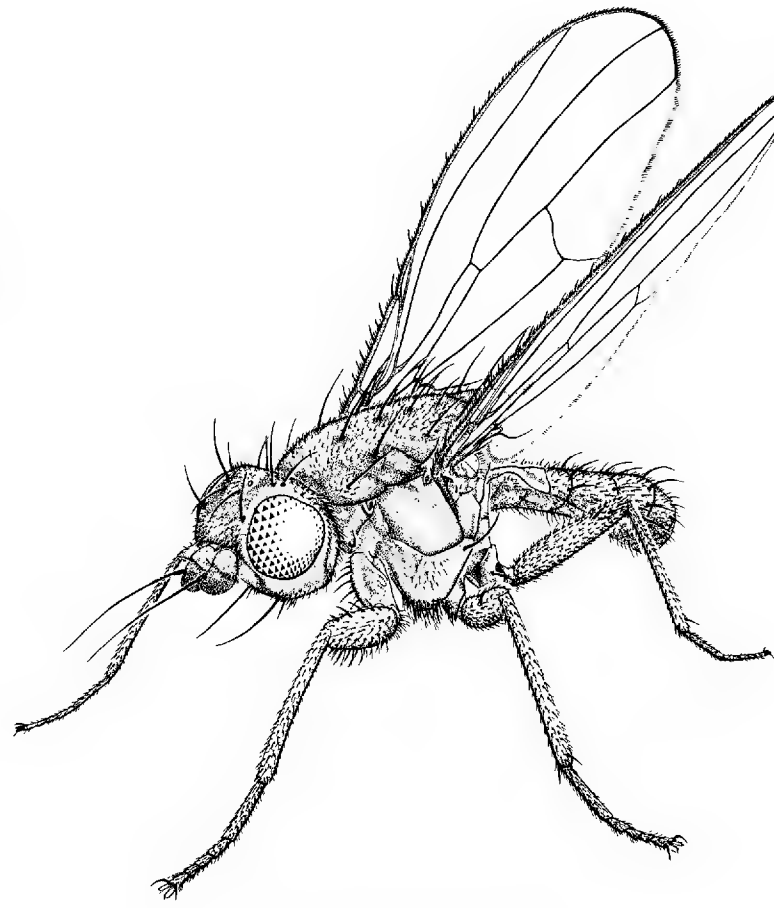
Thorax (Figs 20–26) not strongly arched (see Chapter 12: 317; key couplets 90–91), without intra-alar setae; 0–1 prescutellar acrostichal setae variable; usually with 3–5 pairs of dorsocentral setae; postpronotal seta usually present (absent in

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2021. Manual of Afrotropical Diptera. Volume 3. Brachycera—Cyclorrhapha, excluding Calyptratae. *Suricata* 8. South African National Biodiversity Institute, Pretoria; pp. 2131–2144.

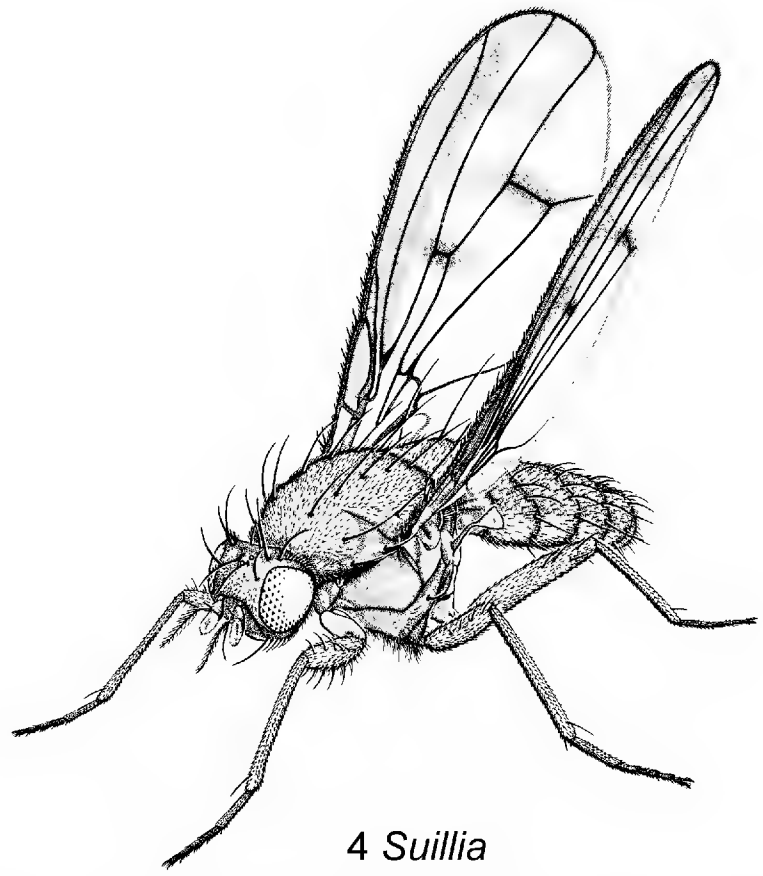
Afrotropical *Suillia* Robineau-Desvoidy) (Fig. 23); 2 notopleural and 3 supra-alar setae present; proepisternal seta usually present (absent in *Suillia*); anepisternum bare or setulose (in Malagasy *Suillia*); katepisternum with 1 or more setae posteriorly (in Cnenospathidinae and Trixoscelidinae), usually with additional anterior and ventral setulae; anepimeron rather bare, sometimes setulose (in *Aberdareleria* Woźnica and *Pseudoleria* Garrett); meron bare; scapular seta present in *Kiboleria* Lindner and *Tephrochlamys* Loew (Figs 20, 25). Scutellum with 2 strong marginal setae, sometimes setulose on disk and between lateral setae (*Suillia*). Wing (Figs 27–34) with membrane hyaline, often with faint yellowish or brownish tinge, rarely mottled with contrasting whitish and dark grey areas, often maculate with crossveins infuscate; costagial break well-developed, positioned where subcostal vein (*Sc*) joins costal vein; costal vein (*C*) extending to vein M_1, usually with conspicuous spines,



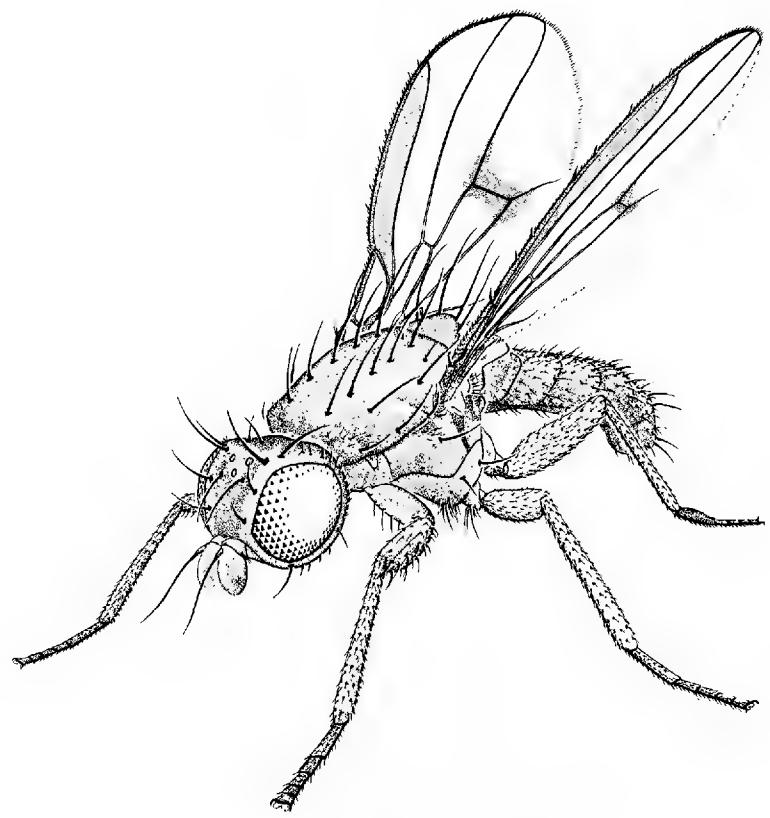
2 *Kiboleria*



3 *Pseudoleria*



4 *Suillia*

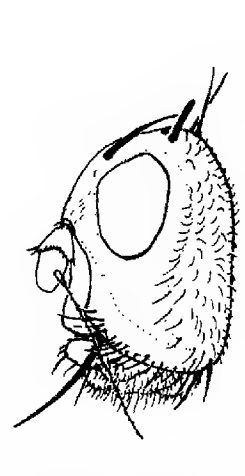


5 *Trixoscelis*

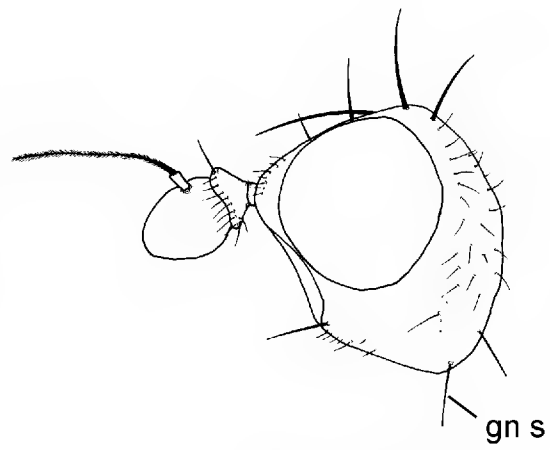
Figs 98.2–5. Habitus of adult Heleomyzidae (dorsolateral views): (2) *Kiboleria* sp.; (3) *Pseudoleria pectinata* Loew; (4) *Suillia* sp.; (5) *Trixoscelis* sp.

especially in larger specimens, variously developed in some taxa; radial veins typically developed; pterostigma (Fig. 28) often present, but never ending behind level of radial–medial crossvein (*r–m*) (in all Afrotropical species); vein *CuA+CuP* short or long, often almost reaching wing margin; cells *bm* and *dm* entirely separated; cell *cua* present. Legs only moderately setose (Figs 2–5), varying among genera and species; mid tibia with 1 or more apical ventral setae; fore, mid and hind tibiae usually with preapical dorsal setae; pulvilli pad-like; empodium seta-like; claws moderately long and stout.

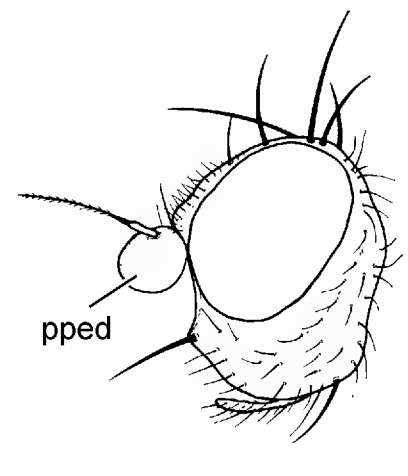
Abdomen narrower than thorax in dorsal view, tapering distally in female (Fig. 36), rather rounded, knob-like in male (Fig. 35); sparsely to moderately setulose; 7 pairs of spiracles usually present in membrane of lateral margins of tergites in both sexes, but those of segments 6 and 7 sometimes displaced in male (Fig. 35); male abdominal segments 1–5 symmetrical; tergites and sternites 6–8 usually variously developed; tergite 6 variable in size, asymmetrical, often reduced, sometimes represented by sclerotised bands or small plates, often displaced to right; usually partially fused with its respective sternite, sometimes as small plate-like remnants freely situated in membrane; in *Kiboleria* and *Tephrochlamys* tergite and sternite 6 symmetrical, often macrotrichose (Heteromyzinae *sensu* Gorodkov 1972; Papp 1998: 441); in *Suillia* greatly reduced; sternites 6 and 7 more or less fused with sternite 8 on left side (in Suilliinae *sensu* Gorodkov 1972; Papp 1998: 440); in *Trixoscelis* Rondani tergite 6 much reduced, but free; sternite 6 reduced and located on left side, separate from partially fused syntergosternite 7 + 8 (Fig. 35) (in Trixoscelididae *sensu* Papp 1998: 432); in *Pseudoleria* tergite 6 reduced to narrow transverse strip; sternites 6 and 7 asymmetrically placed, at least sternite 7 joined to sternite 8 (McAlpine 1985, fig. 66; in all Heleomyzinae *sensu* Papp 1998: 442); tergite 6 rather large and virtually symmetrical, sternites 6 and 7 situated on left side without traces of tergites 7 and 8 in *Prosopantrum* Enderlein (Cnemospathididae *sensu* Papp, 1998: 430); male terminalia with epandrium relatively large, somewhat rounded, but in *Prosopantrum* with rather band-like dorsal part and cranial process on left side (Papp 1998: 430); cercus well-developed, usually at least partially fused, in various shapes; 1 pair of surstyli present, sometimes fused with epandrium (*Prosopantrum*), of various shapes and symmetry; ejaculatory apodeme and gonites present; phallapodeme various in shape and size, fused to hypandrium (*Prosopantrum*, *Pseudoleria* and *Suillia*) or free (*Kiboleria*, *Tephrochlamys* and *Trixoscelis*); female abdomen (Fig. 36) with tergites and sternites distinct; sternite 8 with small, but usually distinct pair of lobes; epiproct and hypoproct distinct, but usually small; cerci free and separated; spermathecae varying



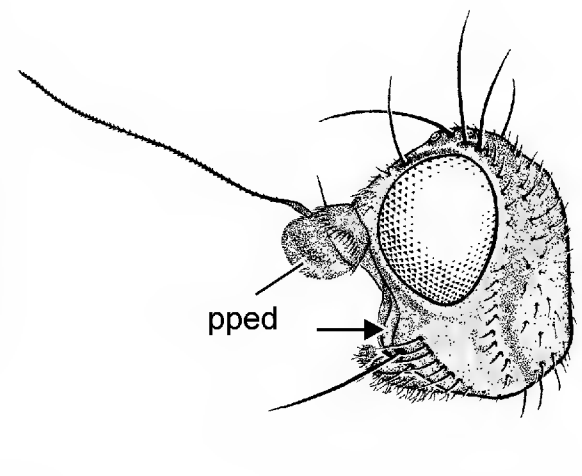
6 *Aberdareleria*



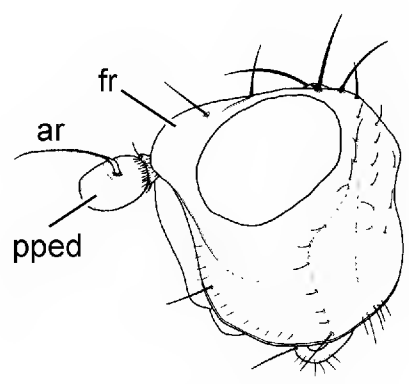
7 *Kiboleria*



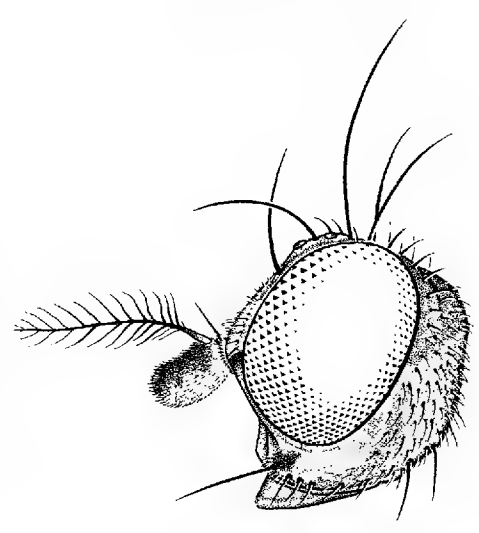
8 *Prosopantrum*



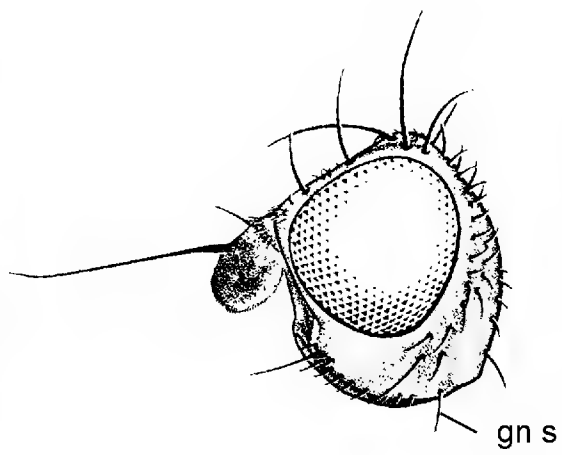
9 *Pseudoleria*



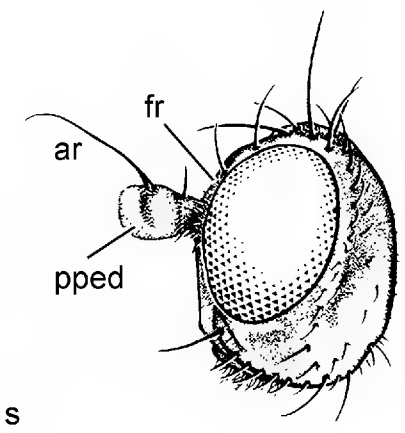
10 *Stuckenbergiella*



11 *Suillia*



12 *Tephrochlamys*



13 *Trixoscelis*

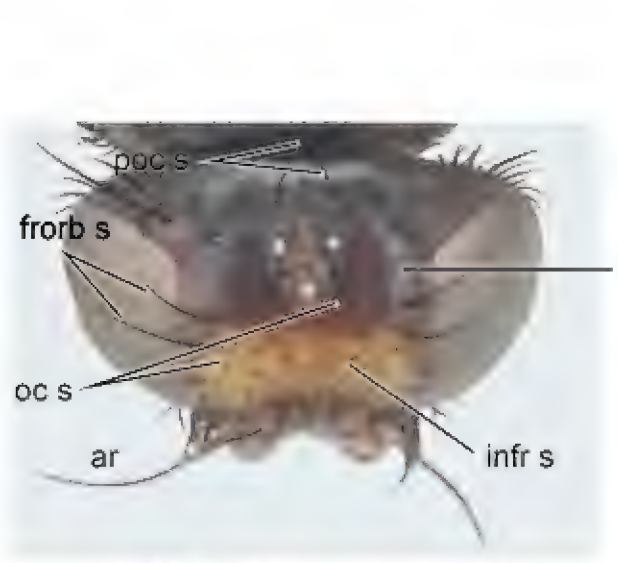
Figs 98.6–13. Heads of Heleomyzidae (lateral views): (6) *Aberdareleria freidbergi* Woźnica; (7) *Kiboleria ugandensis* Cogan; (8) *Prosopantrum flavifrons* (Tonnoir & Malloch); (9) *Pseudoleria* sp. (arrow indicates sclerotised median panel); (10) *Stuckenbergiella littoralis* Cogan; (11) *Suillia* sp.; (12) *Tephrochlamys namibensis* Woźnica; (13) *Trixoscelis* sp. Fig. 6 (after Woźnica 1993, fig. 1), Figs 7, 8, 10 (after Cogan 1971, figs 13, 12, 99, respectively).

Abbreviations: ar – arista; fr – frons; gn s – genal seta; pped – postpedicel.

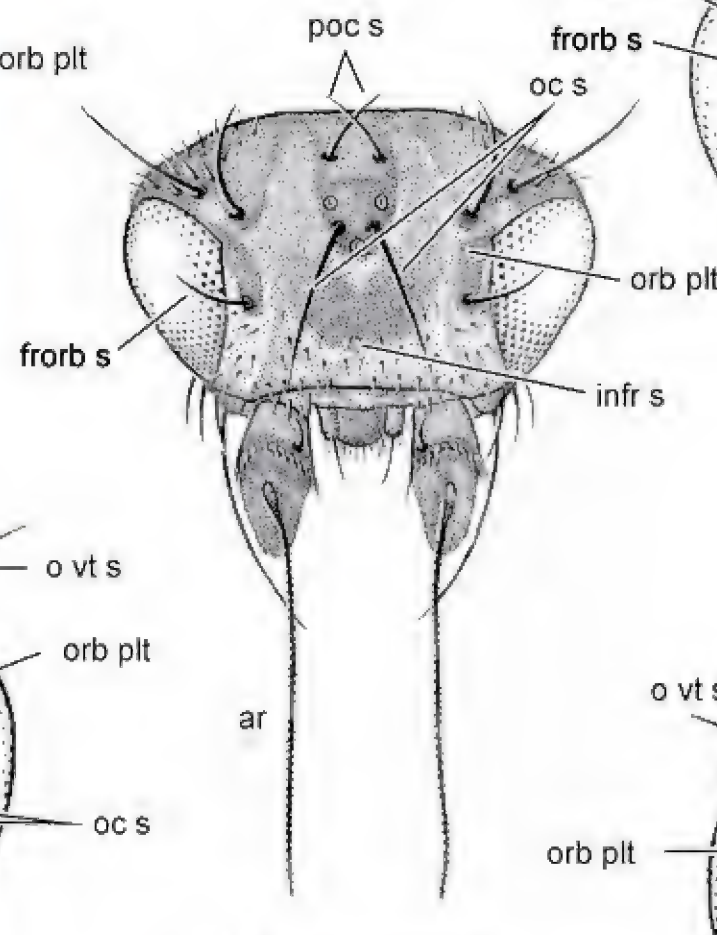
from 2 (some extralimital species) to 4 (in some *Suillia*), usually 3, with one being somewhat removed from the other two (by separate ejaculatory duct), all moderate in size, variously shaped, but heavily sclerotised.

Egg (Fig. 37) whitish, elongate-oval, slightly curved, with reticulated patterning (Fig. 37, inset). Larva of typical cyclorrhaphous form (Fig. 38), with 5 or 6 pairs of tubercles on last abdominal segment caudally; prothoracic spiracle (Figs 38, 39) usually fan-shaped, with 6–14 papillae; posterior spiracle (Figs 38, 40) usually bearing peristigmatic tufts (except in *Suillia*, Fig. 40); cephaloskeleton (Fig. 41) with mouthhooks and intermediate sclerite robustly built; basal sclerite with ventral cornu with subdorsal "window". Puparium (Fig. 42) barrel-shaped, narrowed anteriorly.

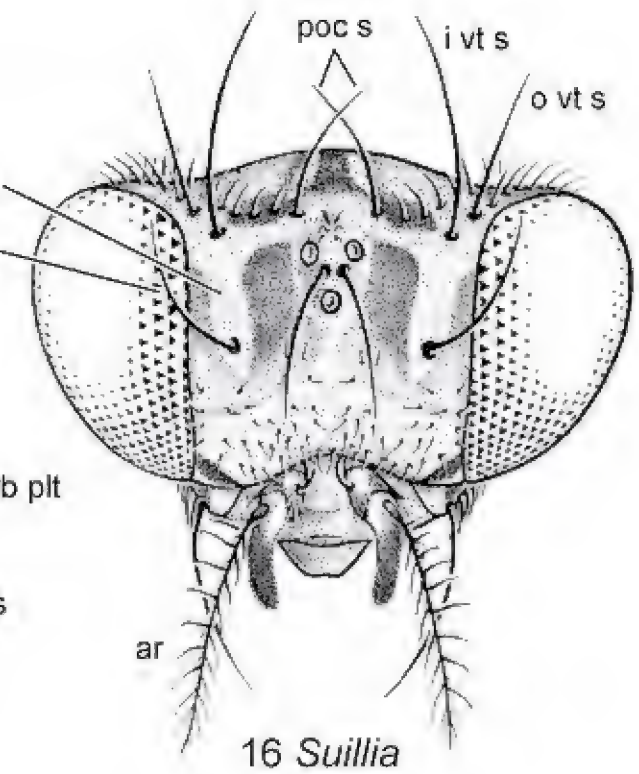
Adult heleomyzids are superficially similar to some Curtonotidae (see Chapter 103), but differ in having 1 or 2



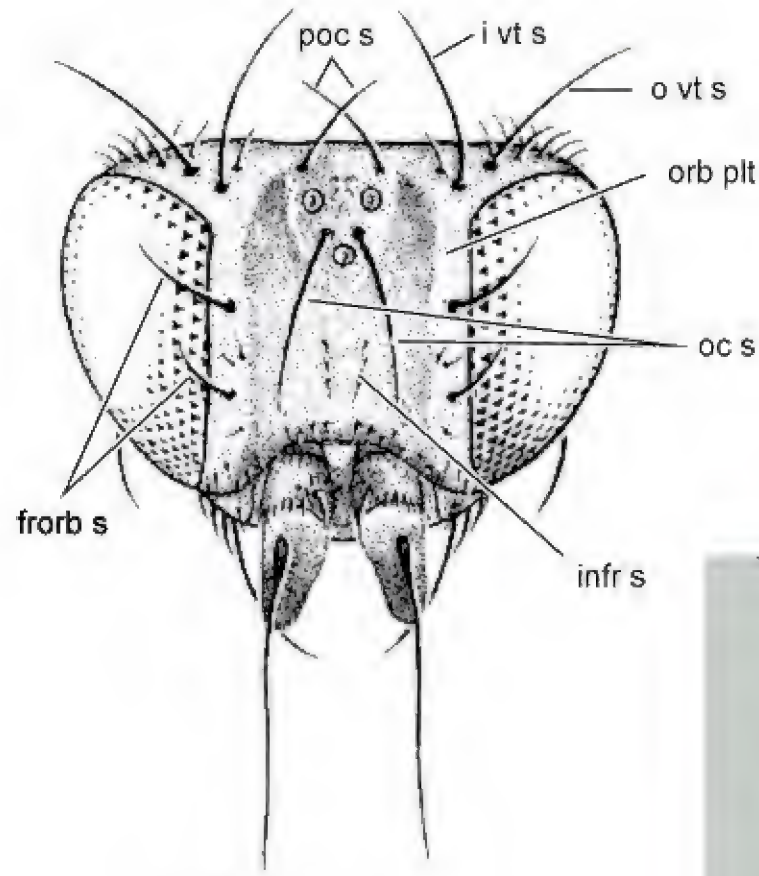
14 *Prosopantrum*



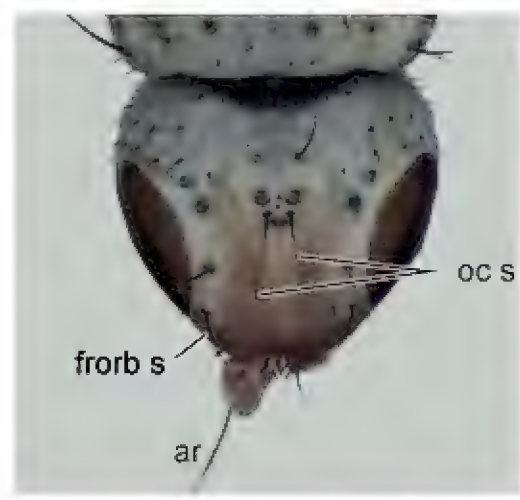
15 *Pseudoleria*



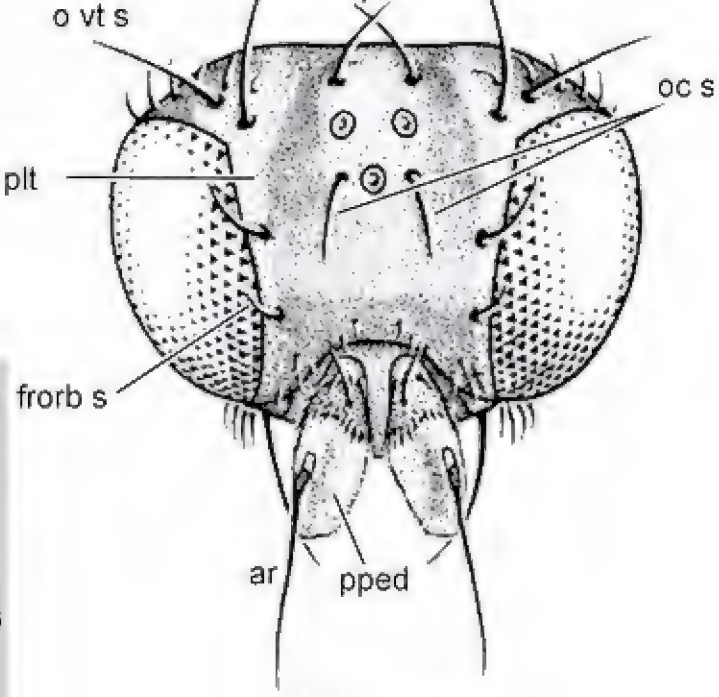
16 *Suillia*



17 *Tephrochlamys*



19 *Stuckenbergiella*



18 *Trixoscelis*

Figs 98.14–19. Heads of Heleomyzidae (dorsal views): (14) *Prosopantrum* sp. (non-Afrotropical); (15) *Pseudoleria* sp. (non-Afrotropical); (16) *Suillia* sp.; (17) *Tephrochlamys namibensis* Woźnica; (18) *Trixoscelis* sp.; (19) *Stuckenbergiella littoralis* Cogan. Figs 14, 19 (© Trustees of Natural History Museum, London).

Abbreviations: ar – arista; frorb s – fronto-orbital seta; i vt s – inner vertical seta; infr s – interfrontal setulae; o vt s – outer vertical seta; oc s – ocellar seta; orb plt – orbital plate; poc s – postocellar seta; pped – postpedicel.

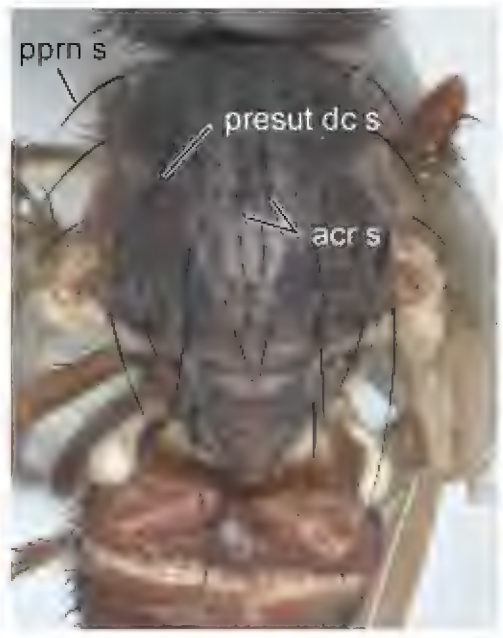
fronto-orbital setae that are never strongly proclinate. They are also similar to some Sphaeroceridae (see Chapter 99), but heleomyzids only have a subcostal break and hind tarsomere 1 is never shorter than tarsomere 2, except in some males of Holarctic species of the tribe Heleomyzini *sensu* Gorodkov (1984: 22).

Biology and immature stages

The biology and ecology of the Heleomyzidae remains poorly understood, the little that is known being summarised by Ferrar (1987: 193) and Smith (1989: 94). Heleomyzid species are largely cold-adapted flies mostly restricted to afforested areas of the Northern Hemisphere, except representatives of the subfamily Trixoscelidinae, which are adapted to xeric, hot sandy and sunny regions. Recently, some data concerning winter activity of Palaearctic Heleomyzidae were published by Boardman (2012) and Soszyńska-Maj & Woźnica (2016), but very little information has been published on diurnal activity, except Okadome (1995), who observed the diurnal prevalence of *Tephrochlamys japonica* Okadome, 1967 and found two peaks of activity: early morning (07:00–10:00) and late afternoon (16:00–19:00). Such activities support representatives of Heleomyzinae (Heleomyzini *sensu* McAlpine 1985) as cold-adapted flies.

Adults of *Prosopantrum* occur on dung and carrion and introduced species of Palaearctic origin are believed to be parthenogenetic, as males have not been found (Cogan 1971). Extralimital species of *Suillia* have also been reared from various mushroom sporophores, but also develop in subterranean

20 *Kiboleria*

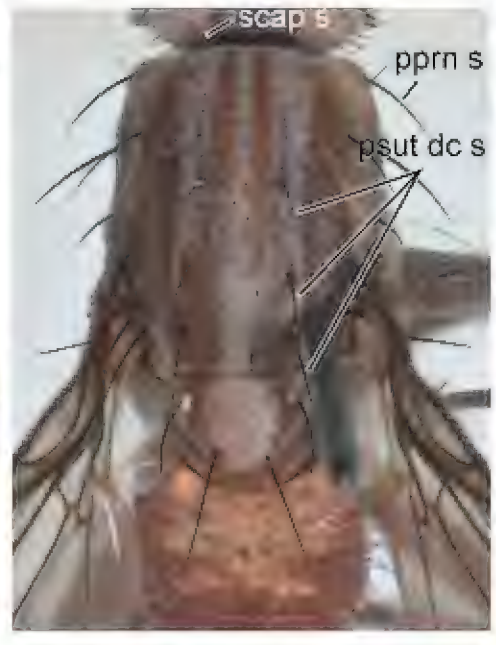


21 *Prosopantrum*

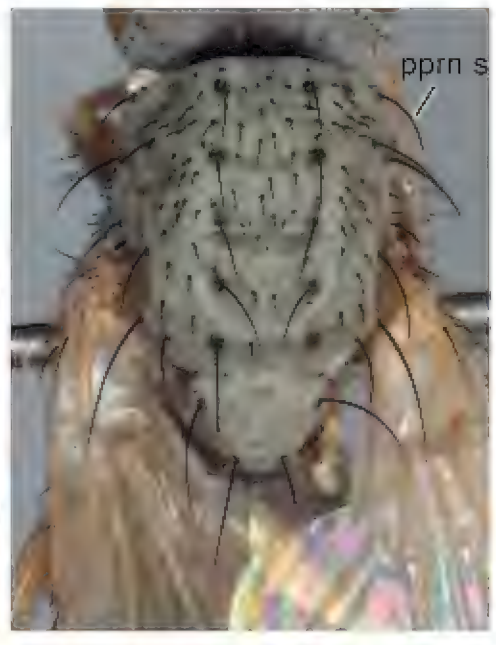
22 *Pseudoleria*

23 *Suillia*

24 *Stuckenbergiella*



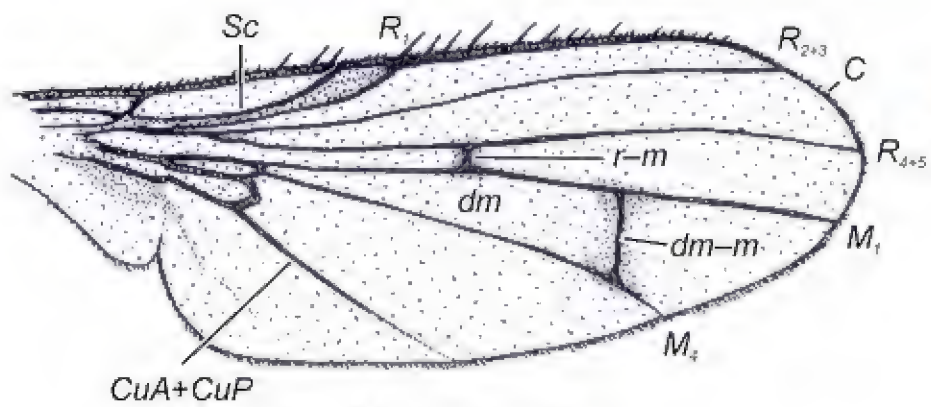
25 *Tephrochlamys*



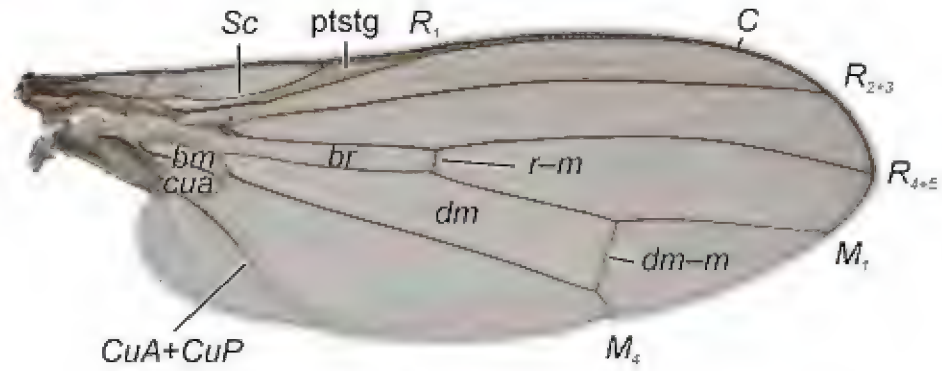
26 *Trixoscelis*

Figs 98.20–26. Mesonota of Heleomyzidae (dorsal views): (20) *Kiboleria lindneri* Cogan; (21) *Prosopantrum* sp. (non-Afrotropical); (22) *Pseudoleria* sp. (non-Afrotropical); (23) *Suillia picta* (Wiedemann); (24) *Stuckenbergiella littoralis* Cogan; (25) *Tephrochlamys madagascariensis* Cogan; (26) *Trixoscelis irrorata* Cogan. Figs 19–25 (© Trustees of Natural History Museum, London).

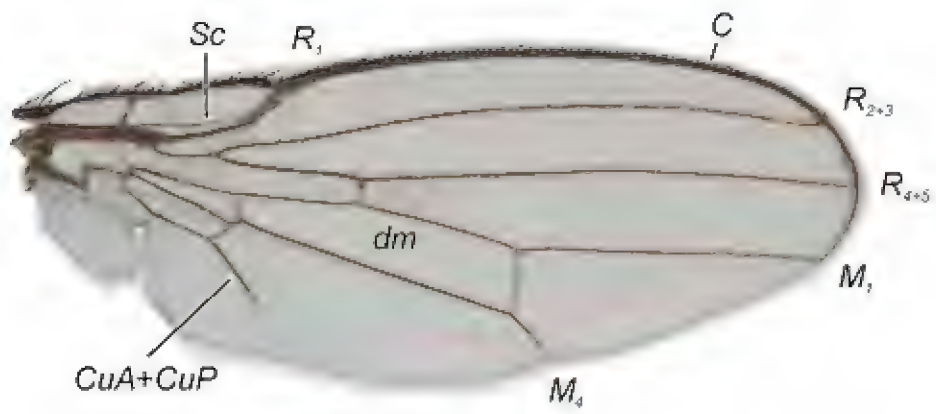
Abbreviations: acr s – acrostichal seta; pprn – postpronotum; pprn s – postpronotal seta; presut dc s – presutural dorsocentral seta; psut dc s – postsutural dorsocentral seta; scap s – scapular seta.



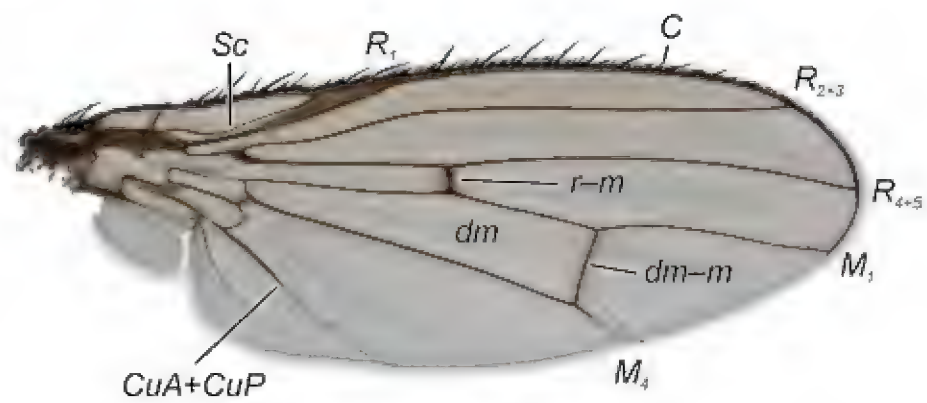
27 *Aberdareleria*



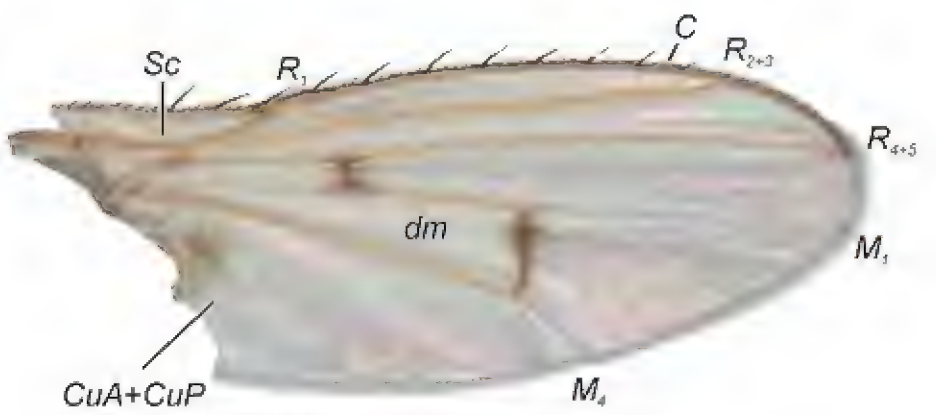
28 *Kiboleria*



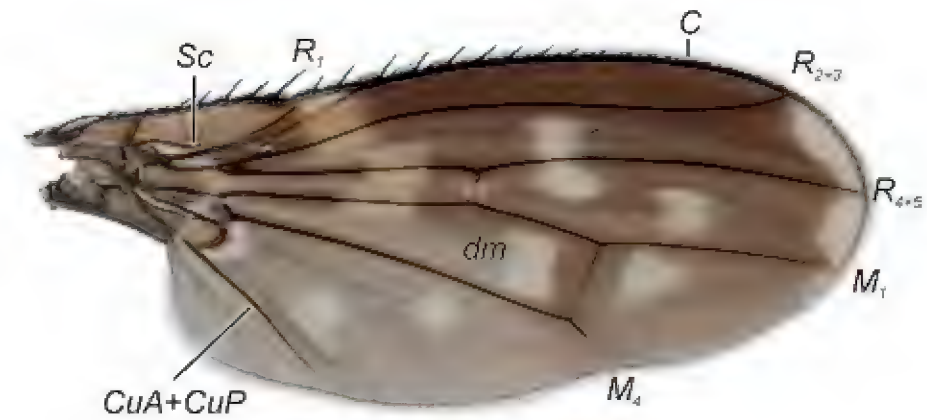
29 *Prosopantrum*



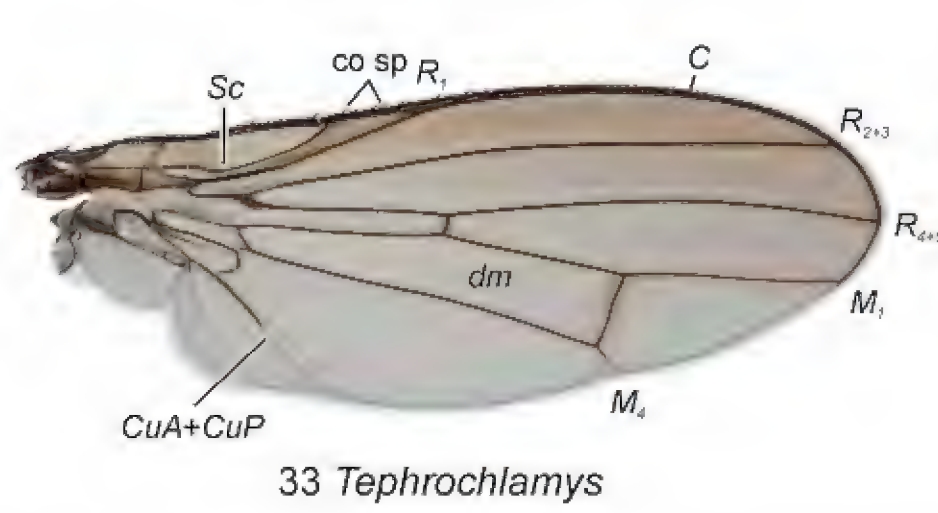
30 *Pseudoleria*



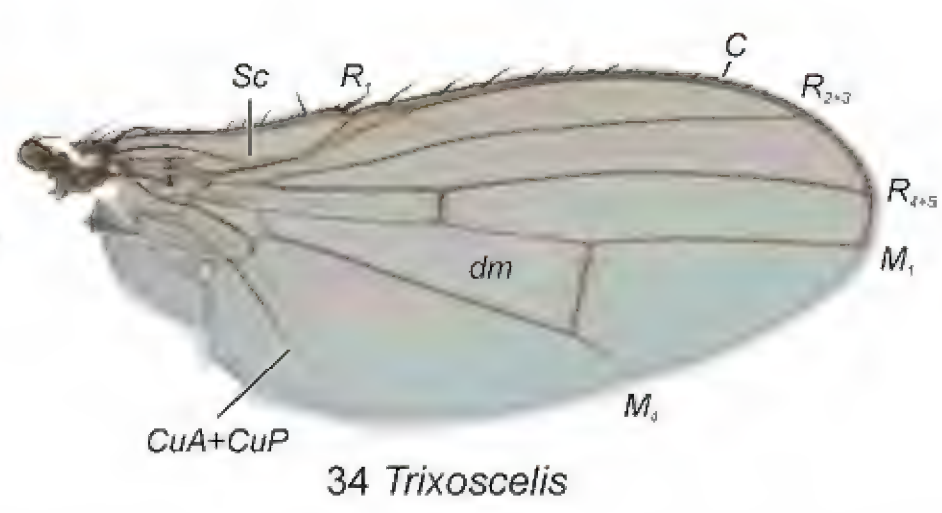
31 *Stuckenbergiella*



32 *Suillia*



33 *Tephrochlamys*



34 *Trixoscelis*

Figs 98.27–34. Wings of Heleomyzidae (dorsal views): (27) *Aberdareleria freidbergi* Woźnica; (28) *Kiboleria lindneri* Cogan; (29) *Prosopantrum* sp. (non-Afrotropical); (30) *Pseudoleria* sp. (non-Afrotropical); (31) *Stuckenbergiella littoralis* Cogan (basal part of wing damaged); (32) *Suillia picta* (Wiedemann); (33) *Tephrochlamys madagascariensis* Cogan; (34) *Trixoscelis irrorata* Cogan. Fig. 27 (Woźnica 1993, fig. 3), Figs 28–34 (© Trustees of Natural History Museum, London).

Abbreviations: *bm* – basal medial cell; *br* – basal radial cell; *C* – costal vein; co sp – costal spines; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *dm* – discal medial cell; *dm–m* – discal medial crossvein; M_1 – first branch of media; M_4 – fourth branch of media; ptstg – pterostigma; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Sc* – subcostal vein.

truffles of the genus *Tuber* (Tuberaceae) and representatives of the *S. lurida/univittata* species-group are regarded as pests of onion and garlic, *Allium* spp. (Amaryllidaceae) (see below). *Suillia ustulata* (Meigen, 1830) has been reared from a dead elder stem and *S. variegata* (Loew, 1862) from roots of *Aster* (Asteraceae) (Smith 1989: 95). Specific premating behaviour of a *Suillia* species on basidiocarps was studied in central Japan (Tuno *et al*. 2003) and a similar behaviour was observed in a Nearctic *Suillia* species (Coin 2014).

Some details of the chorion structure of the egg of Palaearctic Heleomyzidae were published by Gaponov (2004*a*, *b*). Morphological details of the eggs, larvae and puparia were also provided, based on extralimital species, by Ferrar (1987: 193), Gill & Peterson (1987: 974), Gorodkov (1963), Hennig (1952: 252), Lobanov (1970), Papp (1998: 439) and Smith (1989: 201). The egg, third-instar larva and puparium of the Nearctic species, *Pseudoleria placata* (Hutton, 1901) (as *P. crassata*), were re-described by Gill & Peterson (1987: 974), based on the description provided by Garnett & Foote (1967). Papp (1994) described the immature stages of the Palaearctic species *S. pallida* (Fallén, 1820) and re-described those of *S. univittata* (von Roser, 1840), published earlier by Ciampolini & Süss (1983). Rotheray (2012) and Rotheray *et al*. (2016) described the puparia of the Palaearctic species *S. atricornis* (Meigen, 1830), *S. bicolor* (Zetterstedt, 1830), *S. ustulata* and *S. variegata*. Diagnostic characters of the third-instar larvae of the genus *Suillia* (= Suilliinae) were included in the identification key published by Papp (1998: 451). In respect to other genera recorded from the Afrotropics, only a few third-instar larvae have been described for extralimital species of the genus *Tephrochlamys* (Lobanov 1970) and Papp (1998: 451) summarised the known immature stages of Palaearctic Heleomyzidae (*sensu* Gorodkov 1972).

Economic significance

Some Palaearctic *Suillia* species are frequently associated with fungi and decaying plants or are known to attack cultivated onion and garlic (*Allium*), *i.e.*, *S. lurida* (Meigen, 1830) and *S. univittata*, or truffles, *i.e.*, *S. affinis* (Meigen, 1830), *S. gigantea* (Meigen, 1830), *S. humilis* (Meigen, 1830) and *S. tuberiperda* (Rondani, 1867) and could be introduced in other regions through human activity. Some species often occur in houses and adults of *Tephrochlamys* species are of sanitary importance, frequently observed on the walls and windows of lavatories (Okadome 1967).

Classification

Although the Heleomyzidae was long treated as a family of uncertain relationship by Hennig (1958: 624), or a representative of the superfamily Anthomyzoidea (= Anthomyzoinea *sensu* Griffiths 1972: 190), it is now regarded as belonging to the Sphaeroceroidea (McAlpine 1989: 1479). The history of the various rankings and limits of the family have been outlined in Diptera monographs and in other regional Diptera manuals.

McAlpine (1985) included all small groups, for which separate family rankings seemed warranted (Borboropsidae (Griffiths 1972: 200), Chiropteromyzidae (Frey 1952), Cnemospathidae (Enderlein 1938: 655), Heteromyzidae (Griffiths 1972: 135), Notomyzidae (Griffiths 1972: 260), Rhinotoridae (as subfamily of Rhopalomeridae by Williston (1896: 125) and Hendel (1916)) and Trixoscelididae (Hendel 1916)), in a single family, the Heleomyzidae. McAlpine's classification and proposed tribal ranks within the family were not entirely accepted by other workers in the group (*i.e.*, Carlés-Tolrá 2002; Papp 1998; Woźnica 2000, 2007). More recently, in a review of the endemic Australian tribe Borboroidini (Wombat flies), McAlpine (2007) reduced the Heleomyzidae and Sphaeroceridae to the single family Heteromyzidae. To date, no other taxonomists working on sphaerocerid or heleomyzid flies have accepted this proposal, which includes the Sphaeroceridae as one of five newly proposed subfamilies within the Heteromyzidae (*i.e.*, Marshall & Buck 2010: 1165; Marshall *et al*. 2011; McAlpine & Woodley 2010: 1159; Roháček 2015: 618). It should be noted that the presence of two costal breaks in the wing of Sphaeroceridae is a distinct character that clearly separates these from the Heleomyzidae.

Wiegmann *et al*. (2011) presented the most complete phylogeny for Diptera and attempted to estimate a unique comprehensive phylogeny of Diptera to reconstruct relationships among recognised families and higher groups, basing on morphological and molecular data. Unfortunately, the relationship among analysed heleomyzid taxa, presented there and other related Diptera did not resolve the problems regarding the limit and relationship within the family Heleomyzidae (including Sphaeroceridae) *sensu* McAlpine (2007). Hence the systematic classification adopted in this chapter is based on more comprehensive data, including unpublished taxonomic information.

To date, 19 fossil heleomyzid species have been described, representing 11 genera, mostly from Baltic Amber (Evenhuis 1994: 436; Woźnica 2007). Four species are known from the African tectonic plate, namely: *Helomyza humilis* Meunier, 1910 (preocc. by Meigen 1830) from Tanzania (Pleistocene/Holocene); *Leria insatiabilis* Meunier, 1910, from Ghana (Holocene); *L. insaturabilis* Meunier, 1910, from Madagascan Copal (Holocene); and *Leriella crassifemorata* Meunier, 1908, from Zanzibarian Copal (Quaternary). Some characters defining these genera are questionable, however, and all the above-mentioned taxa require revision, based on examination of type specimens.

Identification

The Afrotropical fauna comprises 60 described species in eight genera. Descriptions of the Afrotropical taxa are found in: Bezzi (1908), Cogan (1970, 1971, 1977), Collart (1946, 1948), Lamb (1917), Lindner (1956), McAlpine (1984), Papp (1999), Speiser (1910) and Woźnica (2000, 2001, 2009, 2012). Due to a lack of modern revisionary work the fauna is poorly known and the last complete identification key to genera and species of sub-Saharan Africa was that of Cogan (1971). Papp (1999) revised and keyed Afrotropical *Prosopantrum* and Woźnica (2001) Afrotropical *Tephrochlamys*; the only Afrotropical genera to receive modern treatment. Heleomyzidae are best micro-pinned in the field for later double-mounting (see Chapter 2).

Key to genera of Afrotropical Heleomyzidae

1. Head with orbital plate oblique, medially directed anteriorly, clearly separated from eye margin (Fig. 16); frons with 1 strong fronto-orbital seta (Fig. 16); thorax without postpronotal (Fig. 23) and proepimeral setae; wing vein *CuA+CuP* not reaching wing margin (Fig. 32) . . . . . *Suillia* Robineau-Desvoidy

– Head with orbital plate not oblique, not medially directed anteriorly, running parallel to eye margin (e.g., Figs 14, 15, 17–19); frons usually with 2 fronto-orbital setae (e.g., Figs 14, 17–19), but occasionally with 1 fronto-orbital seta (e.g., Fig. 15); thorax with postpronotal (e.g., Figs 20–22, 24–26) and proepimeral setae; wing vein *CuA+CuP* variable in length (e.g., Figs 27–31, 33, 34) 2

2. Head without interfrontal setulae (e.g., Fig. 18); ocellar setae inserted lateral to anterior ocellus (e.g., Fig. 18) or very close to the anterior ocellus (e.g., Fig. 19) 3

– Head with interfrontal setulae (e.g., Figs 14, 15, 17); ocellar setae invariably inserted between anterior and posterior ocelli (e.g., Figs 14, 15, 17) 4

3. Head with anterior fronto-orbital seta lateroclinate (Fig. 19); ocellar setae inserted very close to anterior ocellus (Fig. 19); frons swollen (Fig. 10); antennal arista short, *ca* 2 × longer than height of postpedicel (Fig. 10); postpedicel rectangular (Fig. 10); wing vein *CuA+CuP* ending well before wing margin (Fig. 31). . . . . *Stuckenbergiella* Cogan

– Head with anterior fronto-orbital seta distinctly reclinate (Fig. 18); ocellar setae inserted in front of level of anterior ocellus, farther apart than centres of lateral ocelli (Fig. 18); frons normally developed, flat (Fig. 13); antennal arista 3 × (or more) longer than height of postpedicel (Fig. 13); postpedicel oval or round (variable in shape); wing vein *CuA+CuP* long, almost reaching wing margin as trace (Fig. 33) . . . . . *Trixoscelis* Rondani

4. Thorax without presutural dorsocentral setae (e.g., Figs 20, 25); head with gena with long anteriorly directed seta posteriorly (e.g., Figs 7, 12); thorax with 1 scapular seta (e.g., Figs 20, 25); mid tibia with 1 ventral apical seta 5

– Thorax with presutural dorsocentral setae (e.g., Figs 21, 22); head with gena without long anteriorly directed seta posteriorly (e.g., Figs 6, 8, 9); thorax without scapular seta (e.g., Figs 21, 22); mid tibia with 2 (or more) ventral apical setae 6

5. Thorax with 2 well-developed, distinct postsutural dorsocentral setae (Fig. 20); wing narrow, with reduced costal spines (Fig. 28) . . . . . *Kiboleria* Lindner

– Thorax with 3 well-developed, distinct postsutural dorsocentral setae (Fig. 25); wing normally developed, with distinct costal spines (Fig. 33) . . . . . *Tephrochlamys* Loew

6. Head with face without sclerotised median panel (Fig. 8); antennal postpedicel with upper edge rounded (Fig. 8); 2 well-developed fronto-orbital setae present (Fig. 14); thorax with well-developed acrostichal setae (Fig. 21); katepisternum with 2 strong setae; wing vein *CuA+CuP* short, ending abruptly well before wing margin (Fig. 29) . . . . . *Prosopantrum* Enderlein

– Head with face with lightly sclerotised median panel (e.g., Fig. 9, arrowed); antennal postpedicel with upper edge angulate (e.g., Fig. 9); if 2 fronto-orbital setae present, then anterior often reduced (Fig. 15); thorax with weakly developed acrostichal setae (e.g., Fig. 22); katepisternum with 1 strong seta; wing vein *CuA+CuP* long, reaching wing margin (e.g., Figs 27, 30) 7

7. Wing crossveins *r–m* and *dm–m* distinctly infuscate (Fig. 27); mid tibia with several setae medially, on anterodorsal, posterodorsal and ventral surfaces; thorax with 1 large and 1 small katepisternal seta; anepimeron bare; female terminalia with cercus with large, horn-like processes and hair-like setulae . . . . . *Aberdareleria* Woźnica

– Wing crossveins *r–m* and *dm–m* hyaline in Afrotropical species; mid tibia without setae (except near apex); thorax with 1 katepisternal seta; anepimeron often setulose (Fig. 22); female terminalia with cercus largely setulose (except in *P. pectinata* (Loew, 1872)), sometimes with small additional spines . . . . . *Pseudoleria* Garrett

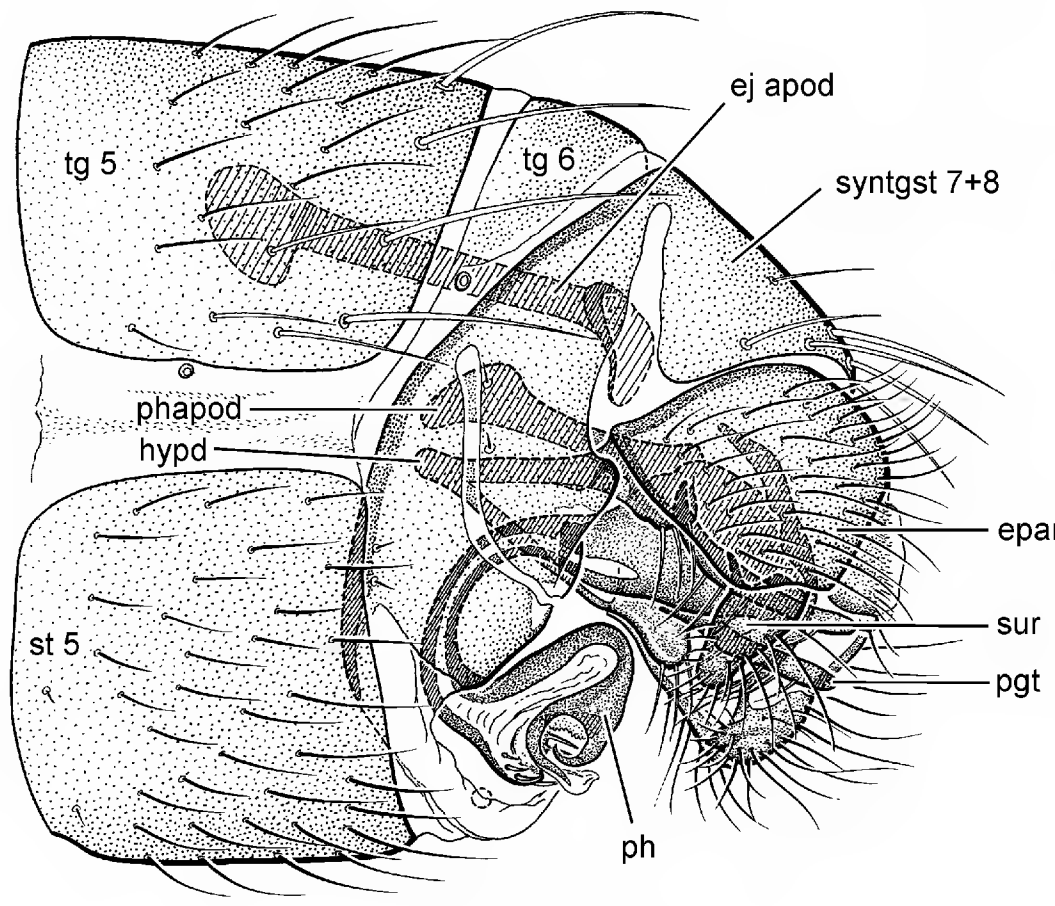
Synopsis on the fauna

***Aberdareleria* Woźnica** (Heleomyzinae: Oecotheini)**.** An endemic monotypic genus, with the single described species, *A. freidbergi* Woźnica, 1993, known from the unique female holotype, described from the Aberdare Mountains, Kenya, at an elevation 3,000–4,000 m. The species is characterised by the rather high head, with numerous setae; the pubescent antennal arista; the wide gena; the bare prosternum; the meron with 1–2 small black setulae; and absence of prescutellar setae (Woźnica 1993). In *A. freidbergi* the female cercus is strongly pigmented, with thorn- and hair-like setae and the spermathecae have a small appendix with the basal parts sclerotised. The genus is probably closely related to the non-Afrotropical genus *Oecothea* Haliday *in* Curtis, but in this genus the cercus bears setulae only and the spermathecae are round

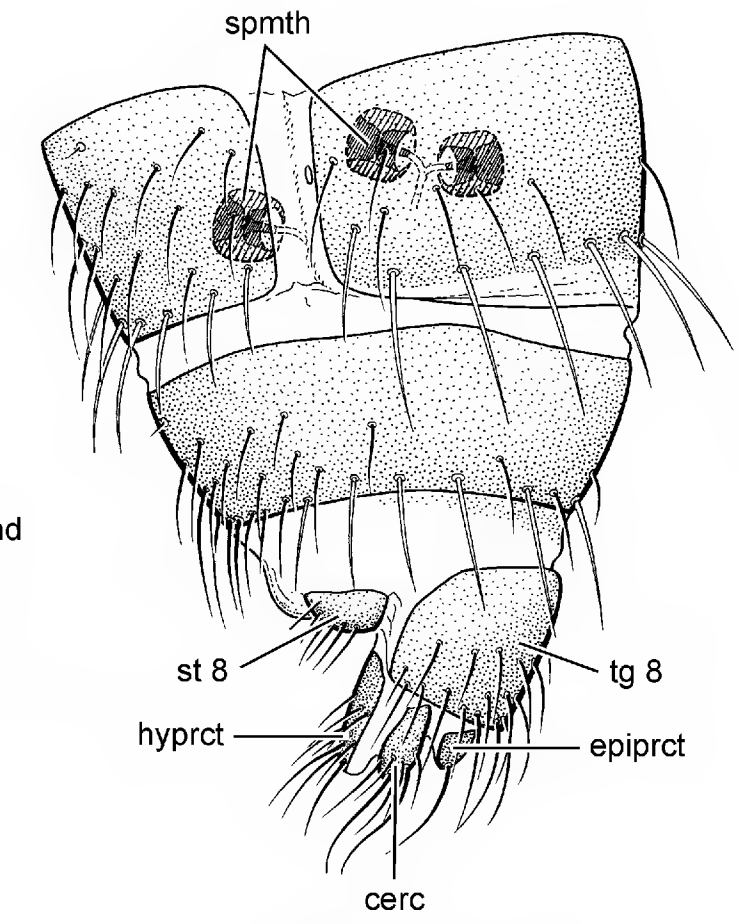
and unsclerotised in their basal parts (Gorodkov 1959). Morphological characters indicate that the species probably occurs in small mammal (rodent) burrows, where the saprophagous larvae likely develop. The male biology and immature stages remain unknown. *Aberdareleria freidbergi* is a cryptic inhabitant of moorlands in montane areas. The head is illustrated in Fig. 6 and the wing in Fig. 27. The species can be identified by reference to Woźnica (1993).

***Kiboleria* Lindner** (Heleomyzinae: Heteromyzini *sensu* Woźnica 1998)**.** An endemic genus of four described species (Fig. 2): *K. edwardsi* Cogan, 1971, from Kenya and Uganda; *K. lindneri* Cogan, 1971, from Yemen; *K. silvaepluvialis* Lindner, 1956, from Tanzania; and *K. ugandensis* Cogan, 1971, from Uganda. A few additional Afrotropical species await description. The genus is characterised by two well-developed and distinct postsutural dorsocentral setae and narrow wings, with reduced costal spines. The structure of the male and female terminalia strongly supports *Kiboleria* as being sister-group to *Tephrochlamys* (Cogan 1971), known from the Old World and the Nearctic. The distribution of all known and undescribed species of *Kiboleria* confirm Cogan's (1971) suggestion that it is a montane genus, only occurring at high elevations (1,980–4,200 m). The biology and immature stages remain unknown. The head is illustrated in Fig. 7 and the wing in Fig. 28. An identification key to all described species was provided by Cogan (1971).

***Prosopantrum* Enderlein** (Cnemospathidinae: Cnemospathidini)**.** A genus of 15 nominal species occurring in the Afrotropical, Australasian/Oceanian, Neotropical and Palaearctic Regions (Malloch 1933: 199; Papp 1999), which is probably native to Africa and South America. Afrotropical species were reviewed by Papp (1999, as Cnemospathididae) and the fauna currently comprises four species: *P. acrostichale* Papp, 1999, from Nigeria; *P. congolense* Papp, 1999, from Republic of Congo; *P. demeteri* Papp, 1999, from Nigeria (all of which are probability native to the Afrotropics); and *P. flavifrons* (Tonnoir & Malloch, 1927), which is introduced into South Africa. Papp's (1999) revision was based on very limited material and additional species should be expected following more extensive sampling in the region. Species of the genus are relatively uniform in general appearance and identification may be problematic, especially in the case of female specimens. The genus can be characterised by: the face missing the sclerotised median panel (typical for Heleomyzini *sensu* McAlpine 1985); the gena broad; the mesonotum with 3 or 4 pairs of strong acrostichal setae (not developed in other Afrotropical genera); the wing with costal spines weak; the male terminalia with the surstylus fused to the epandrium; the phallus extremely long, flexible and ribbon-like, with highly complicated structures apically; the gonopods asymmetrical (unique in Heleomyzidae); the female postabdomen extremely long, with 3 unique spermathecae (Papp 1999); and the cerci short but separate. *Prosopantrum flavifrons*, described from New Zealand, but widespread also in Australia, South America and South Africa (Cogan 1971), has been collected from the English coast (Cole 1996; Ismay & Smith 1996) and from Nordeney Is. (Germany) in the Palaearctic (Stuke & Merz 2005). Cogan (1971)



35 *Trixoscelis* ♂



36 *Trixoscelis* ♀

Figs 98.35–36. Male and female terminalia of Heleomyzidae: (35) male terminalia of *Trixoscelis flavida* Melander, lateral view (non-Afrotropical); (36) same, female terminalia. Figs 35, 36 (Teskey 1987, figs 4, 5).

Abbreviations: cerc – cercus; ej apod – ejaculatory apodeme; epand – epandrium; epiprct – epiproct; hypd – hypandrium; hyprct – hypoproct; ph – phallus; pgt – postgonite; phapod – phallapodeme; spmth – spermathecae; st – sternite; sur – surstylus; syntgst – syntergosternite; tg – tergite.

noted that as all specimens recorded outside South America were females and the species may be capable of reproducing parthenogenetically outside its natural range. Adults have been found on human faeces and on carrion (Cogan 1971; Papp 1999), but the biology and immature stages otherwise remain unknown. The head is illustrated in Fig. 8 and the wing in Fig. 29. An identification key to the four Afrotropical species was provided by Papp (1999).

***Pseudoleria* Garrett** (Heleomyzinae: Oecotheini)**.** A genus of 12 described species (Fig. 3) native to the Nearctic Region, with two species, *P. pectinata* and *P. placata*, introduced into the Australasian/Oceanian Region (McAlpine 1984). *Pseudoleria pectinata* was also introduced into the Afrotropical Region, where the species is recorded from South Africa (Cogan 1980: 611) and more recently from the United Arab Emirates in the Afrotropical part of the Arabian Peninsula (Woźnica 2008: 680). The species was also introduced into Palaearctic North Africa (Egypt) (Weele 2001; Woźnica 2008: 681). The genus is characterised by the very small anterior orbital seta, often reduced in the male; and the bare prosternum and anepisternum. The female of *P. pectinata* is quite distinct from other *Pseudoleria* species, in having a thick patch of short setulae on each side of abdominal tergite 3 (Gill 1962). Larvae of this species feed on rodent droppings and human faeces, as do other representatives of *Pseudoleria*, and have been introduced to some tropical regions with high human activity. The head is illustrated in Fig. 9 and the wing in Fig. 30. The species can be identified by reference to McAlpine (1984) and Woźnica (2008).

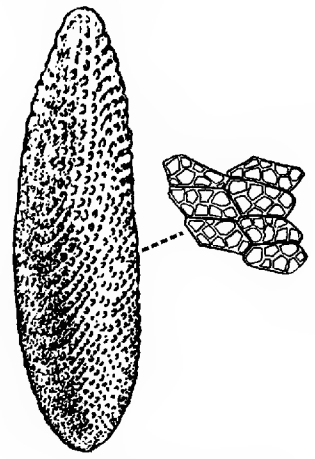
***Stuckenbergiella* Cogan** (Trixoscelidinae: Trixoscelidini)**.** An endemic monotypic genus, with the single described species, *S. littoralis* Cogan, 1971, described from coastal South Africa (Cogan 1971). The species superficially resembles the genus *Tethinosoma* Malloch from New Zealand, which McAlpine (1967) transferred to the family Canacidae (subfamily Tethininae). The species exhibits several adaptions to littoral habitats, including reduction of the antenna and eyes, general arrangement of the thoracic and leg chaetotaxy and the mid and hind tarsomeres have long and strong ventral setulae, probably to aid locomotion on sandy coastal substrates (Cogan 1971). *Stuckenbergiella littoralis* is a rare cryptic inhabitant of coastal regions of the Indian Ocean and is only recorded from two localities (Kasoua and Port Alfred in the Eastern Cape Province). The male, biology and immature stages remain unknown. The head is illustrated in Fig. 10 and the wing in Fig. 31. The species can be identified by reference to the description of Cogan (1971).

***Suillia* Robineau-Desvoidy** (Heleomyzinae: Heleomyzini)**.** One of the largest genera of Heleomyzidae (Figs 1, 4), with *ca* 130 described species, occurring in all zoogeographical regions except the Australasian Region and Antarctica, being especially speciose in the Northern Hemisphere. The genus is also the most widely distributed group in the Afrotropical Region, with 19 recognised species (Cogan 1980: 611; Woźnica 2012). All Afrotropical species, except the widely distributed *S. picta* (Wiedemann, 1830), are confined to high, afforested mountain ranges, where the climate is more moderate and larvae can develop in basidiomycete fungi (Cogan 1971, 1977; Woźnica 2012). Adult morphology, including the structure of the male and female terminalia, is well-described and illustrated in the various monographs and papers concerning the genus, e.g., Cogan 1971; Czerny 1924; Gill & Peterson 1987; Woźnica 2006, 2012. The genus can be characterised by: the presence of one fronto-orbital seta; the postpronotal and proepimeral setae are absent; the male terminalia with the phallus comparatively short, characteristically asymmetrical, composed of a low number of asymmetrical sclerites (Papp 1998: 440); and the females with two separate spermathecal ducts having 1 + 2 or 2 + 2 spermathecae. Although other characters point to the genus *Suillia*, two Afrotropical species, namely *S. immaculata* Czerny, 1924 and *S. wittei* (Collart, 1946), represent a sub-group and differ in having four pairs of dorsocentral setae only (1 + 3), as opposed to the normal 1 + 4. Two species with distinctly maculate wings and dark body colouration are distributed across several African countries. *Suillia picta* is a common species in Southern Africa and its close relative, *S. ingens* (Lamb, 1917) (Fig. 1), is known from five African countries in Central and East Africa (Cogan 1971, 1980: 612). Only one species, *S. variegata*, occurs widely outside the Afrotropics and is common along the Mediterranean and elsewhere in Europe. The occurrence of *S. griseola* (Meigen, 1830) (= *similis* (Meigen 1838)) in Kenya, as recorded by Cogan (1971), is unconfirmed and this species was removed from the Afrotropical list by Woźnica (2012). Within *S. aspinosa* (Lamb, 1917), Cogan (1971; 1980: 612) recognised four subspecies (keyed as subspecies by Cogan 1971), but these have subsequently been found to differ from one another in chaetotaxy, body colouration and the structure of the male terminalia and should be regarded as valid species (Woźnica 2012). One species, *S. keiseri* Cogan 1971, endemic to Madagascar, bears 1–2 large anepisternal setae, a condition also present in one Neotropical species (*S. iniens* Giglio-Tos, 1893) and this character was regarded as a homoplasy shared by two distant species by Woźnica (2006). No immature stages are known based on Afrotropical species and *S. variegata* is the only species occurring in the region, for which the puparium has been described, based on specimens from Europe (Rotheray 2012; Rotheray *et al.* 2016). Relatively few third-instar larvae have been described in detail for the genus as a whole and all are based on Palaearctic species (Ciampolini & Süss 1983; Nikolova 1962; Papp 1994, 1998: 451). The head is illustrated in Fig. 11 and the wing in Fig. 32. An identification key to Afrotropical species was provided by Cogan (1971) and Woźnica (2012) provided replacements to Cogan's key couplets 18–20, to include *S. stuckenbergi* Woźnica, 2012.

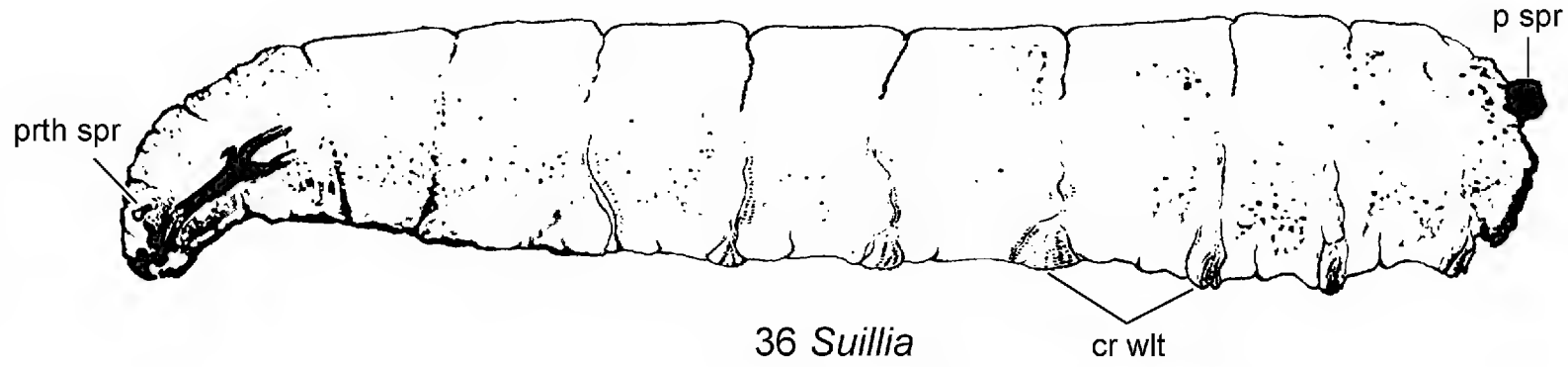
***Tephrochlamys* Loew** (Heleomyzinae: Heteromyzini)**.** A genus of ten described species occurring in the Afrotropical and Oriental Regions and Holarctic Realm (Woźnica 2001). One species, *T. rufiventris* (Meigen, 1830), which is widely distributed in the Holarctic, was recorded from New Zealand by Pitkin (1989: 597), but this record requires verification. Three species occur in the Afrotropics: *T. australis* Cogan, 1971, widely distributed in South Africa; *T. madagarsariensis* Cogan, 1971, from Comoros and Madagascar; and *T. namibensis* Woźnica, 2001, described from Namibia (Woźnica 2001). The biology and immature stages of Afrotropical species remains unknown, but are probably similar to those described by Lobanov (1970) and Rotheray (2012). The saprophagous larvae of *Tephrochlamys* occur in decaying fungi, mouldy dead wood, carrion, dung and other decomposing matter (Smith 1989: 95) and adults occur in the vicinity of the larval breeding media,

including birds' nests, caves, dead wood, *etc.*, mostly in shaded areas. The head is illustrated in Fig. 12 and the wing in Fig. 33. An identification key to Afrotropical species was provided by Woźnica (2001).

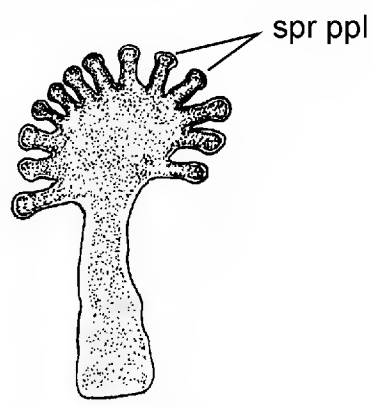
Trixoscelis **Rondani** (Trixoscelidinae: Trixoscelidini)**.** One of the largest genera of Heleomyzidae (Fig. 5), with over *ca* 130 species, occurring in all zoogeographical regions, except Australasia and Antarctica. Only one (apparently undescribed) species has been examined from the Oriental Region and the majority of previously described Neotropical species were formally treated as the genus *Spilochroa* Williston (Cogan 1977). Thirty species are recorded from the Afrotropical Region, mostly restricted to Southern Africa (chiefly from Namibia and South Africa) (Cogan 1971, 1977, 1980: 612; Woźnica 2000, 2009). Cogan (1977) noted that in the Afrotropical fauna the most extensive speciation appears to have taken place in the xeric areas of south-western Africa, especially in the Namib Desert region and its margins. In a study of species restricted to the Brandberg massif on the margins of the Namib Desert, for example, Woźnica (2000) recorded five described species of the genus and described four more. One species is, however, known from the more mesic KwaZulu-Natal Province, South Africa and another from Zambia (Cogan 1977). One species, *T. phylacis* Séguy, 1953 described from Mauritania, was synonymised by Woźnica (2009), with the common Mediterranean species *T. puncticornis* (Becker, 1907), which is widely distributed on the coast of the Mediterranean basin and is



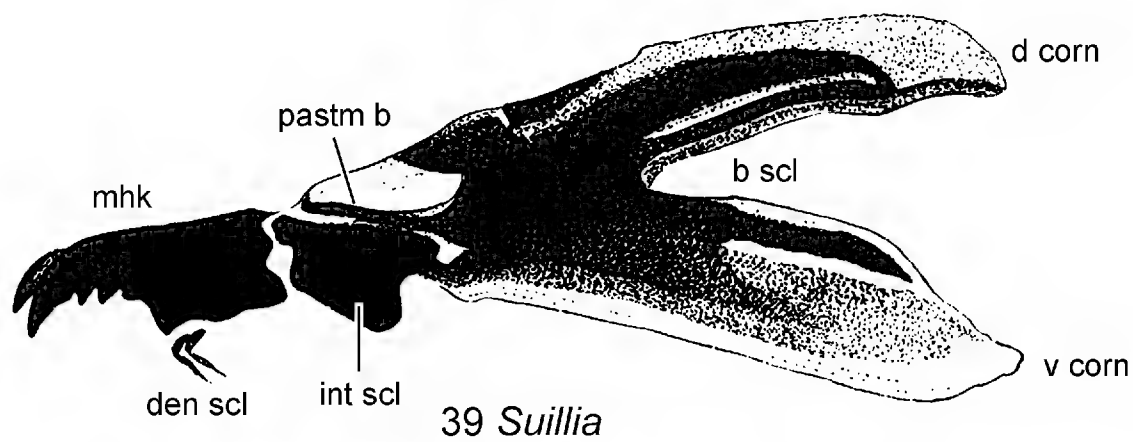
35 *Suillia*



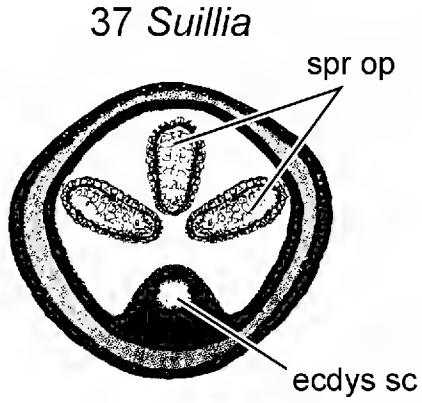
36 *Suillia*



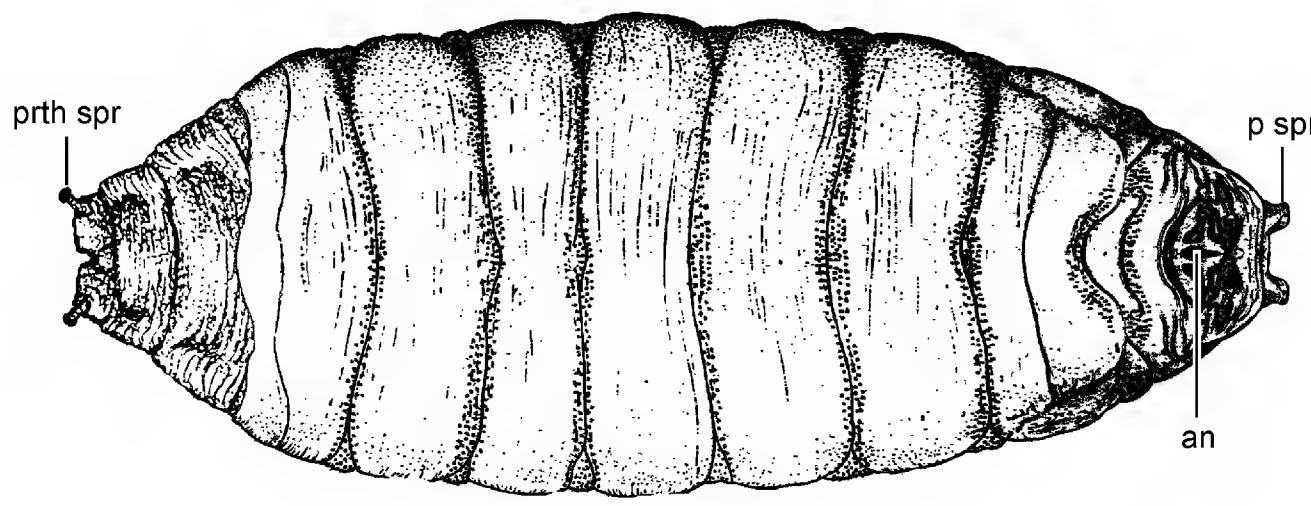
37 *Suillia*



39 *Suillia*



38 *Suillia*



40 *Suillia*

Figs 98.37–42. Immature stages of Heleomyzidae (all non-Afrotropical): (37) egg of *Suillia univittata* (von Roser), lateral view (inset: detail of chorion surface); (38) same, third-instar larval habitus, lateral view; (39) same, larval prothoracic spiracle, dorsal view; (40) same, larval posterior spiracle, caudal view; (41) same, larval cephaloskeleton, lateral view; (42) same, puparial habitus, ventral view. Figs 37, 39–41 (after Nikolova 1962, figs 1, 5, 3, 4, respectively), Fig. 38 (after Papp 1998, fig. 63), Fig. 42 (after Ciampolini & Süss 1983, fig. 20).

Abbreviations: an – anus; b scl – basal sclerite; cr wlt – creeping welts; d corn – dorsal cornu; den scl – dental sclerite; ecdys sc – ecdysial scar; int scl – intermediate sclerite; mhk – mouthhook; p spr – posterior spiracle; pastm b – parastomal bar; prth spr – prothoracic spiracle; spr op – spiracular openings; spr ppl – spiracular papillae; v corn – ventral cornu.

further recorded from similar places in North Africa (Tunisia), Azores Is. and Canary Is. and from United Arab Emirates in the Afrotropical part of the southern Arabian Peninsula. Studies of recent material, especially from Namibia, indicate that a large number of species (*ca* 20–30) probably await discovery and description. The most recent revision of Nearctic species also resulted in the description of 13 new species among 38 nominal taxa (Foster & Mathis 2011). These authors also redefined the geographical range of the genus, generic synonymy and provided a modern diagnosis. *Trixoscelis* is closely related to the endemic monotypic Afrotropical genus *Stuckenbergiella*, differing in head chaetotaxy, with two pairs of reclinate orbital setae (Figs 10, 13, 18). Foster & Mathis (2011) mentioned that the gena-to-eye ratio of various *Trixoscelis* species ranges from 0.15–0.55, whereas in *Stuckenbergiella* the ratio is greater than 1.0. The genus can be characterised by the anepisternum invariably with one or two strong setae at the posterodorsal corner, along with only three or four much smaller setulae in a cluster; the presence of two katepisternal setae, sometimes three, but then the genal setulae near the vibrissa are also enlarged (a single vibrissae in *Stuckenbergiella*); the female terminalia with tergite and sternite 7 clearly fused; and the presence of three strongly sclerotised, variously shaped spermathecae. *Trixoscelis* species occur on vegetation or flowers in hyper-arid or arid, shrubby areas, grasslands and coastal sand dunes. They commonly come to light and at least some species are crepuscular or nocturnal. The biology and immatures stages otherwise remain unknown, although Smith (1989: 95) noted that the extralimital species *T. canescens* (Loew, 1865) was reared from the nest of a Common blackbird, *Turdus merula* L., and from soil derived from Feral pigeon, *Columba livia domestica* Gmelin, guano. The head is illustrated in Fig. 13 and the wing in Fig. 34. Afrotropical species can be identified using the identification keys provided by Cogan (1971, 1977) and Woźnica (2009), supplemented by reference to the original descriptions of Woźnica (2000).

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SPHAEROCERIDAE 99

(Lesser Dung Flies)

László Papp† and Jindřich Roháček

Fig. 99.1. Male of *Gymnometopina* sp. (South Africa) (photograph © S.A. Marshall).

Diagnosis

Small-sized (body length: 0.7–5.5 mm), robust acalyptrate flies (Figs 1–7), best diagnosed by short, dilated hind tarsomere 1 (Figs 54–56); colour brown to blackish, sometimes with yellow, orange, or reddish head, thorax, legs and/or markings; head, thorax and abdomen sometimes with characteristic micro-tomentose pattern; wings sometimes maculate (Figs 3, 17, 19) and legs variegated.

Head (Figs 8–19) at most as wide as thorax (except in some apterous and short-winged species and some non-Afrotropical Homalomitrinae), usually higher than long; frons (Figs 26–28) broad, slightly tapered anteriorly; fronto-orbital plates more sclerotised than frontal vittae and ocellar triangle well-defined (Fig. 26); frontal triangle less distinctly delimited (Fig. 26); occiput convex to slightly concave; lunule (Figs 26–28) distinctly developed; face broad medially, forming keel-like facial carina (Fig. 28) and dorsolaterally shallow to deep antennal foveae; some genera of Sphaerocerinae (*Lotobia* Lioy and *Ischiolepta* Lioy) and Homalomitrinae (*Sphaeromitra* Roháček & Marshall), with dorsally expanded epistoma (Fig. 28); gena variable, broad in small-eyed species (Fig. 31); vibrissal angle more or less distinctly developed (except in Homalomitrinae and Sphaerocerinae); chaetotaxy (Figs 26, 27) with postocular setae usually short, convergent, cruciate or absent (Figs 26–28); outer vertical, inner vertical and ocellar setae normally long (Figs 26, 27), outer occipital and inner occipital setae usually shorter (all or some of these setae reduced or absent in Homalomitrinae and Sphaerocerinae) (Fig. 27); typically 2 (often only 1) lateroclinate fronto-orbital setae and row of 2–12 inclinate interfrontal setae on frontal vitta usually distinct (Fig. 27);

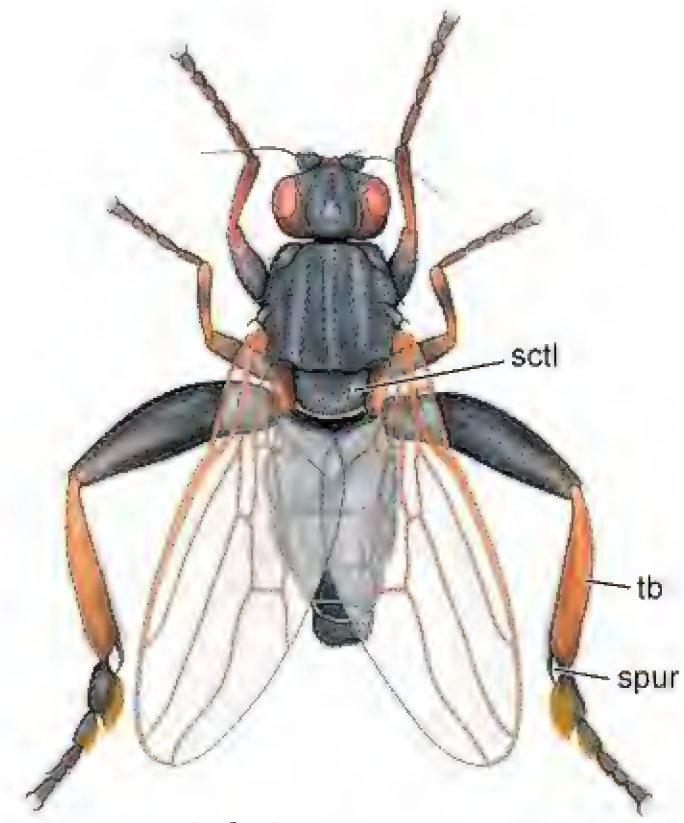
frons sometimes with additional shorter setae or setulae between interfrontal setae and fronto-orbital setae (inner fronto-orbital setulae), near fronto-orbital setae (additional setulae) and on or at posterior margin of ocellar triangle (inner ocellar setulae enlarged in some genera, Fig. 27); postocular setulae at posterior eye margin in 1 or more rows; 1 long vibrissa usually present (Figs 26, 27) and 1 or 2 shorter subvibrissae at vibrissal angle (all reduced or absent in some Sphaerocerinae, Figs 28, 29); gena often with proclinate to upcurved genal seta and some setulae behind it (Fig. 30); a row of peristomal setulae at ventral margin of gena also developed; compound eye variable, sometimes reduced (Figs 30, 31); antenna (Figs 32, 33)

Figs 99.2–7. Photographs of living Afrotropical Sphaeroceridae: (2) *Dudaia* cf. *steineri* L. Papp & Norrbom ♀ (Madagascar); (3) *Giraffimyiella giraffa* (Richards) ♀ (Tanzania); (4) *Poecilosomella* cf. *pallidimana* (Duda) ♀ (Madagascar); (5) *Leptocera caenosa* (Rondani) ♀ (Czech Republic); (6) *Norrbomia* sp. ♂ (left) (Tanzania); (7) adult *Ceroptera* sp. on *Pachylomera femoralis* Kirby (Coleoptera: Scarabaeidae) (South Africa). Figs 2–4, 6, 7 (photographs © S.A. Marshall), Fig. 5 (photograph © J. Roháček).

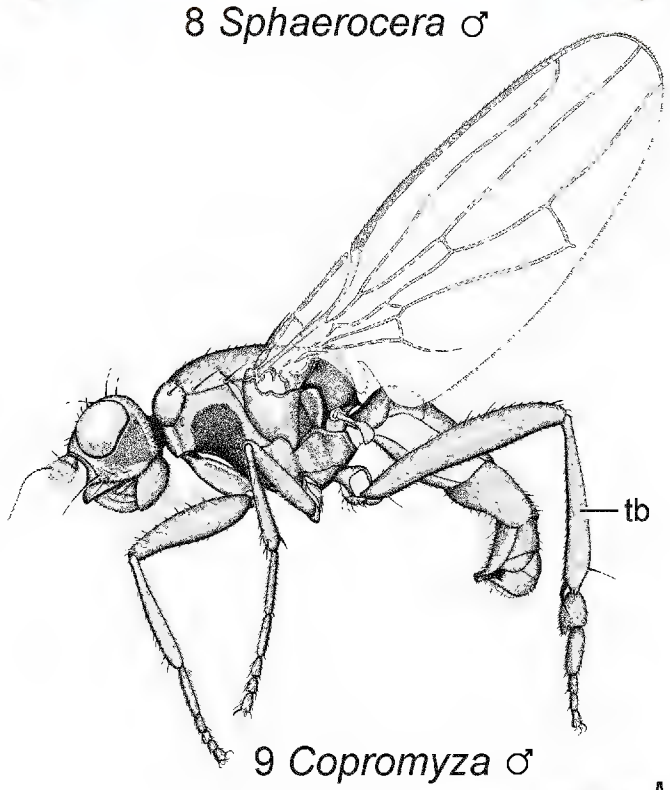
short, only arista long; scape (Fig. 32) usually very small (except for Homalomitrinae); pedicel (Figs 30, 31) longer and conical; postpedicel (Figs 31, 32) usually rounded (rarely apically pointed) and laterally somewhat compressed; arista (Figs 31, 32, 33) dorsopreapical, rarely subapical or apical, almost bare (Sphaerocerinae) to long-branched (plumose); proboscis stout; palpus usually short and slender, with a few fine setulae.

Thorax (Figs 34, 35) with scutum usually setose (in most Sphaerocerinae setae greatly reduced and inserted on warts); postpronotum well-defined (Fig. 35); transverse suture only distinct laterally (Fig. 35); prosternum linear to widened posteriorly (mostly in terricolous species); anepisternum, katepisternum and anepimeron usually distinctly delimited; thoracic chaetotaxy (Fig. 35), with 1 or 2 long postpronotal setae; 2 notopleural setae; 1 or 2 presutural supra-alar setae; 1 postsutural supra-alar seta; 1–3 postalar setae; 1–6 dorsocentral setae (0–3 presutural, 1–3 postsutural); acrostichal setae (Fig. 35) short, in 2–12 rows, between dorsocentral setae on suture; sometimes some (presutural or prescutellar) acrostichal setae enlarged forming macrosetae; anepisternum at most with small setulae (in Homalomitrinae, Sphaerocerinae and Australasian *Pleuroseta* Richards (Limosininae)); katepisternum with 0–3 katepisternal setae at dorsal margin, plus fine ventral setulae; anepimeron usually bare (setulose in Homalomitrinae). Scutellum (Figs 36–39) rounded subtriangular (Fig. 37), trapezoidal (Figs 38, 39), or semicircular (Fig. 36), shortened and transverse in some apterous taxa, with 0–8 (typically 2) pairs of marginal scutellar setae (Fig. 37), in some Sphaerocerinae with 2–20 (or more) marginal teeth (Figs 10, 34); scutellar disc bare (Fig. 36) or setulose (Figs 37–39). Wing (Figs 40–53) moderately broad, narrower in Copromyzinae (Fig. 42) and Sphaerocerinae (Fig. 51), broader in most Limosininae (Figs 40, 41, 43–50, 52, 53); some species with wing shortened, with reduced venation, or fully apterous (Figs 23–25); wing polymorphic in some; membrane usually unicolourous (Figs 9, 10, 16), less often maculate (Figs 3, 4, 17, 19), or with infuscate areas (Figs 18, 47); costal vein (C) with costagial, humeral and subcostal breaks (Figs 41, 42); first costal sector (basicosta to apex of vein R_1) often with enlarged setae, sometimes most of costal vein with erect setulae perpendicular to alar plane (e.g., *Elachisoma* Rondani); costal vein (C) extending to apex of vein M_1 in Copromyzinae (Fig. 42), Sphaerocerinae (Fig. 51) and non-Afrotropical Tucminae, but only to (or slightly beyond) apex of vein R_{4+5} in Limosininae (Figs 44–47) and Homalomitrinae; only Sphaerocerinae retain most complete (ancestral) venation (Fig. 51), with both veins M_1 and M_4 extending to wing margin and with closed basal medial (*bm*) and anterior cubital (*cua*) cells; in Copromyzinae and Tucminae vein M_4 shortened, not reaching wing margin (Fig. 42), but otherwise wing venation resembling that of Sphaerocerinae; in Homalomitrinae and Limosininae venation further reduced (Figs 44–50), with only short appendages of veins M_1 and M_4 beyond cell *dm* and with open cells *bm* and/or *cua*; alula usually well-developed (Fig. 43). Legs (Figs 54–62), relatively stout; femora and tibiae usually with strong and often numerous setae (Figs 57, 59–62); fore and hind femora sometimes strongly swollen; mid trochanter, fore, mid and hind tarsomere 1 sometimes also with characteristic setae or spines; hind tarsomere 1 (Figs 54–56) invariably short and widened; hind tarsomere 2 somewhat thickened, but longer (Fig. 55); rarely all tarsomeres dilated and flattened (*Aspinilimosina* L. Papp and Homalomitrinae).

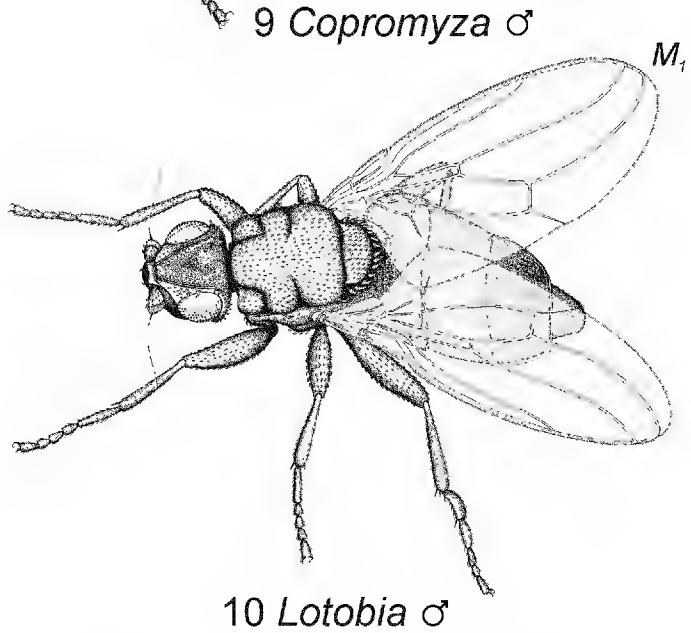
Abdomen with preabdomen (segments 1–5) of both sexes with broad, well-defined tergites; sternites usually much smaller (Fig. 77), sometimes greatly reduced, partly de-sclerotised or broken in several small plates; several genera of Limosininae with strongly reduced tergites (Fig. 77), a convergent feature in different lineages; tergite 1 more or less fused with tergite 2; sternite 1 reduced or absent; female normally with 7 pairs of spiracles in membrane near ventral margin of tergites; male with 6 pairs of spiracles, with spiracle 7 on left side being enclosed, together with spiracle 6 in synsternite 6 + 7; male sternite 5 (Figs 63–71), although formally part of the preabdomen, functionally belongs to male terminalia, often modified to form anterior part of genital pouch and provided with special armature; in some species (e.g., non-Afrotropical *Apteromyia* Vimmer and *Lotobia*) sternite 4 also modified; postabdomen (segments 6–11) asymmetrical (Figs 77, 79); tergites 6–8 normally absent (tergite 6 only present in Tucminae); sternite 6 short, located left lateroventrally and more or less fused with sternite 7 (situated on left side) to form with it synsternite 6 + 7 (Fig. 79); sternite 8 positioned dorsally, usually less asymmetrical and partly fused with sternite 7, sometimes also with epandrium (Fig. 79); male external terminalia (Figs 85–89) composed of large, saddle-shaped epandrium, reduced hypandrium and usually greatly modified or reduced cerci; epandrium sometimes with ventrolateral cleft (most Copromyzinae) or secondarily divided into 2 (anterior and posterior) parts (Sphaerocerinae); epandrium usually symmetrical, less often (in some Neotropical genera of Limosininae) asymmetrical, always with discrete (normally symmetrical) surstyli at ventral margin (Figs 83, 85, 101); surstylus usually with two-point articulation: anteriorly with epandrium and hypandrium, posteriorly (Fig. 81), with subepandrial sclerite *via* its ventrally projecting arms; surstylus sometimes divided into anterior and posterior part and often highly complex, with 2 or more lobes, a number of projections, keels, spines, *etc.* (Figs 85, 91–96); hypandrium relatively small, posteriorly open (thus without posterior hypandrial bridge), V-shaped (Fig. 105) or Y-shaped in ventral view (Fig. 106), with lateral arms free, connected or fused with epandrium; cerci highly variable, often entirely fused with epandrium, forming posteroventral subanal plate enclosing with it sub-oval anal fissure; more rarely cerci large and discrete (Fig. 90), ventrally projecting (Fig. 111) or absent (Fig. 83); epandrium of *Leptocera* Olivier and *Rachispoda* Lioy with additional posterior medial projections of unknown origin, termed pseudocerci (derived from cerci, epandrium or both, Fig. 84); internal terminalia (Figs 113–117), formed of unpaired, free, rod-like phallapodeme; basiphallus normally shorter, heavily sclerotised, often provided with posterior epiphallus or pre-epiphallus or both (Fig. 117); distiphallus larger and usually symmetrical; ejaculatory apodeme usually small (Fig. 115); postgonites paired, free, normally simple and symmetrical, but sometimes complex and rarely asymmetrical (e.g., *Paracuminiseta* L. Papp, Fig. 86 and non-Afrotropical *Puncticorpus* Duda, Fig. 113); pregonites reduced to minute remnants coalesced with basal part of postgonites and connecting these to hypandrium; female preabdomen (segments 1–5) usually with narrower sternites and sternite 5 unmodified; postabdomen (segments 6–11) (Figs 126–130) ranging from long and telescopic (Copromyzinae, Sphaerocerinae and some Limosininae) to short and robust (most Limosininae); tergite 6 sometimes, tergites 7 and 8 often partly de-sclerotised, subdivided or otherwise modified; sternite 7 and, particularly,



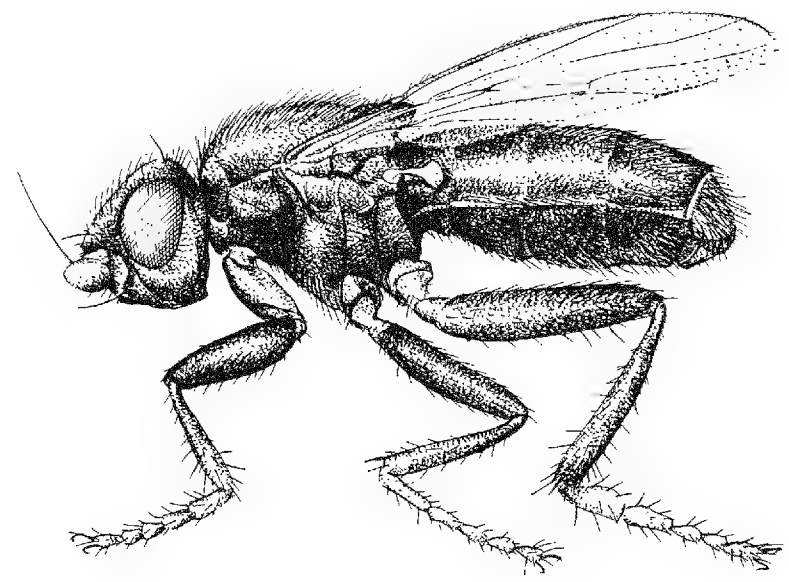
8 *Sphaerocera* ♂



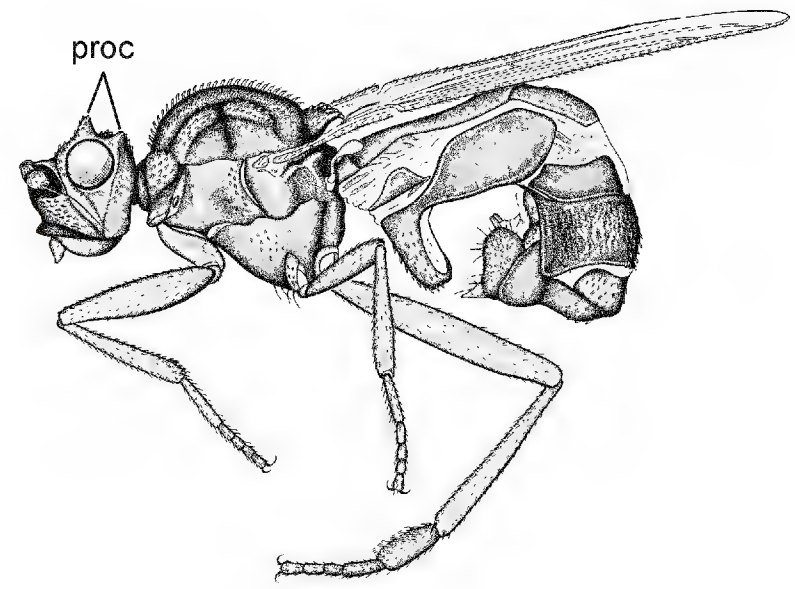
9 *Copromyza* ♂



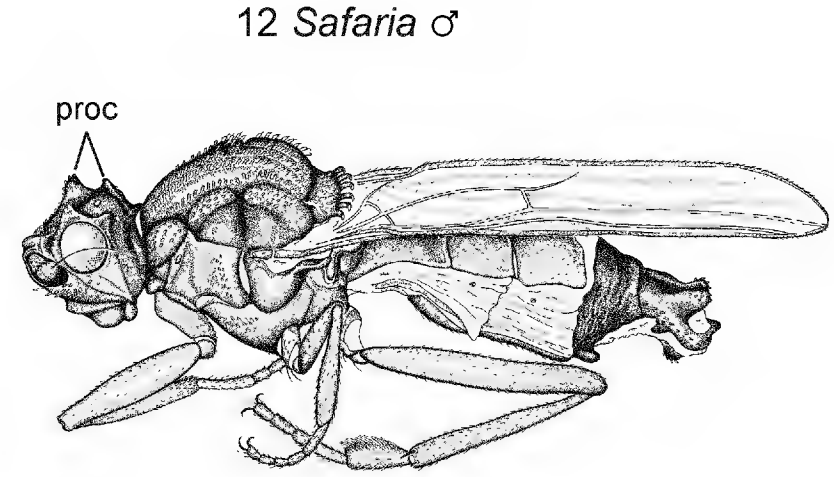
10 *Lotobia* ♂



11 *Trichosphaerocera* ♂



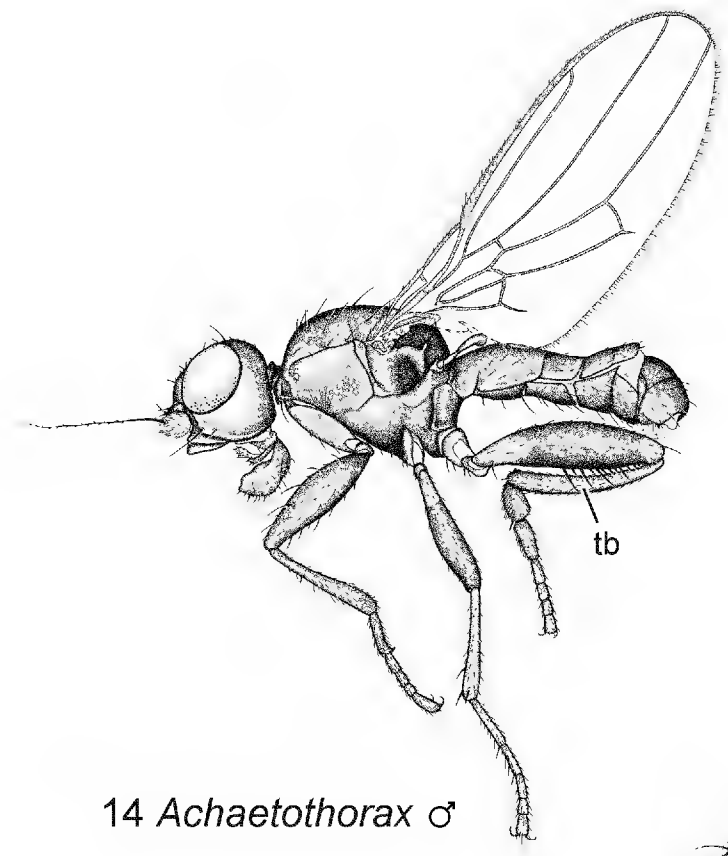
12 *Safaria* ♂



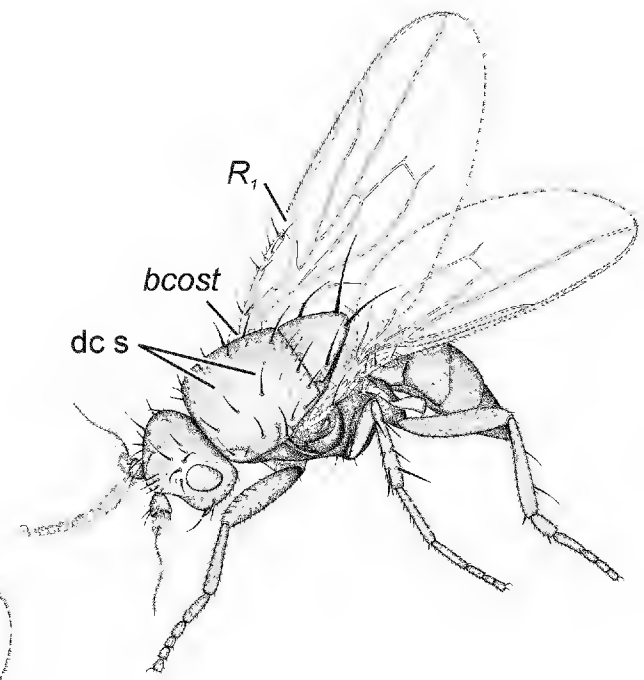
13 *Safaria* ♀

Figs 99.8–13. Habitus of Sphaeroceridae: (8) *Sphaerocera curvipes* Latreille, dorsal view ♂; (9) *Copromyza equina* Fallén, lateral view ♂ (non-Afrotropical); (10) *Lotobia pallidiventris* (Meigen), dorsolateral view ♂; (11) *Trichosphaerocera africana* L. Papp, lateral view ♂; (12) *Safaria forcipata* Richards, lateral view ♂; (13) same ♀. Figs 8, 9, 10, 12, 13 (Roháček *et al*. 2001, figs 9, 5, 7, 8 below, 8 above, respectively), Fig. 11 (Papp 1978, fig. 35).

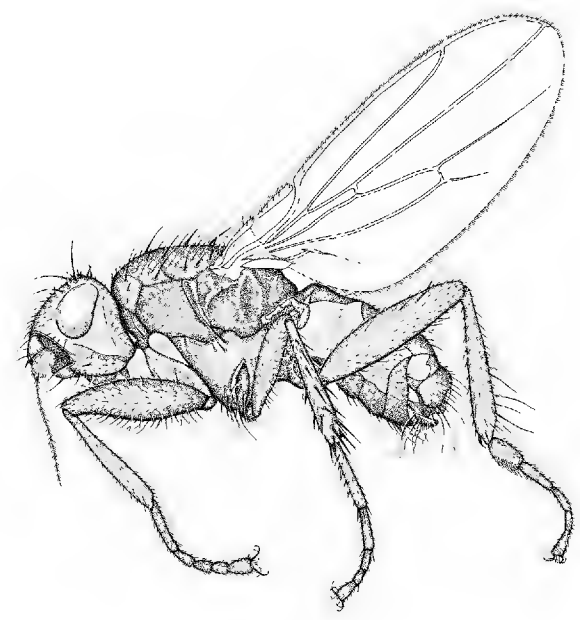
Abbreviations: M_1 – first branch of media; proc – processes; sctl – scutellum; spur – spur; tb – tibia



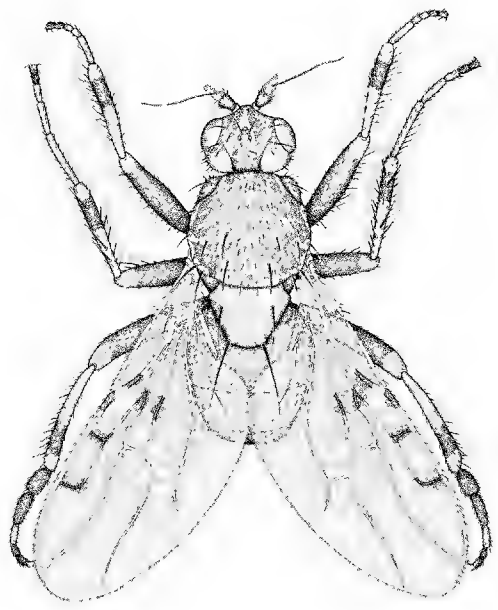
14 *Achaetothorax* ♂



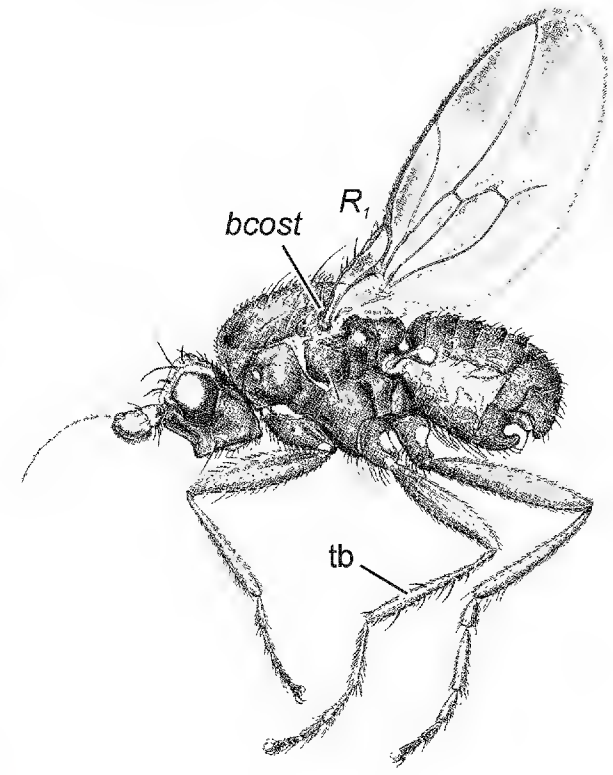
15 *Thoracochaeta* ♀



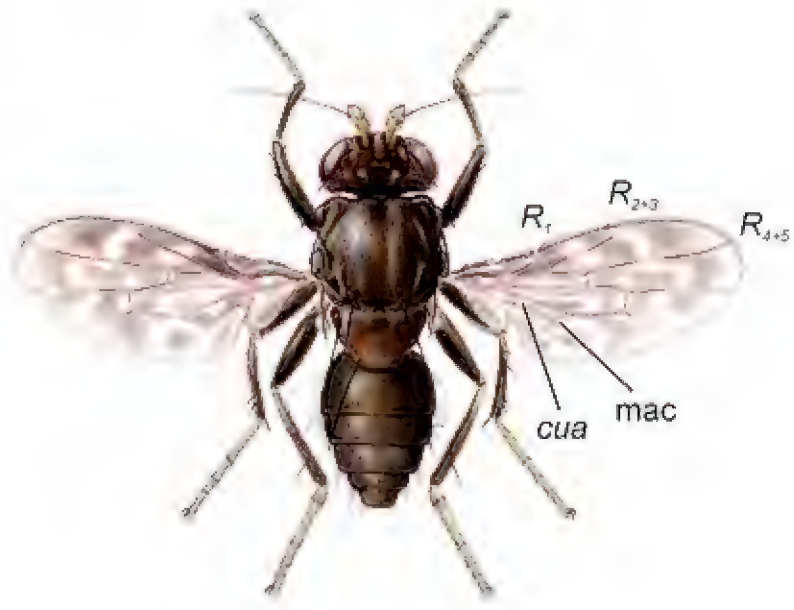
16 *Ceroptera* ♂



17 *Poecilosomella* ♂



18 *Acuminiseta* ♂



19 *Giraffimyiella* ♂

Figs 99.14–19. Habitus of Sphaeroceridae: (14) *Achaetothorax concavus* Norrbom & L. Papp, lateral view ♂; (15) *Thoracochaeta zosterae* (Haliday), dorsolateral view ♀; (16) *Ceroptera setigera* Vanschuytbroeck, lateral view ♂; (17) *Poecilosomella mirabilis* (Vanschuytbroeck), dorsal view ♂; (18) *Acuminiseta ceropteroides* L. Papp, lateral view ♂; (19) *Giraffimyiella giraffa* (Richards), dorsal view ♂. Figs 14, 15, 16, 17 (Roháček *et al*. 2001, figs 2, 26, 14, 22, respectively), Figs 18, 19 (Papp 2008*b*, figs 233, frontispiece).

Abbreviations: *bcost* – basicosta; *cua* – anterior cubital cell; dc s – dorsocentral setae; mac – macula; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; tb – tibia.

sternite 8 often specifically formed, broken into small discs, greatly reduced and/or provided with distinctive spines or pigmentation; an additional sclerite (which can be further divided) may occur between sternites 8 and 10 (Fig. 129), derived from one of these sclerites; also gonopore sometimes surrounded by spines or secondary sclerotisation; abdominal segment 8 often with internal sclerotisation of female genital chamber, usually forming so-called "spectacles-shaped" sclerite, possessing 2 lateral rings (Figs 131, 132); with 3 spermathecae (most Limosininae) or 2 (Copromyzinae and Sphaerocerinae, rarely also in some genera of Limosininae, e.g., *Bitheca* Marshall), variable in form and surface sculpture (Figs 134–138), most commonly vesicular or sub-globular, often with apex either invaginated or evaginated; epiproct (tergite 10) (Figs 126, 127) usually small, plate-shaped, with pair (or more) of dorsal setae, rarely bare, extended and/or heavily sclerotised; hypoproct (sternite 10) (Figs 126–130) rather variable, usually reduced or partly de-sclerotised; cerci (Figs 126–130) normally simple, formed as setulose lobes, sometimes reduced or fused with hypoproct, provided with thick apical spines, rarely transformed to heavily sclerotised projections.

Egg (Figs 139, 140) relatively large 0.2–1.2 mm in length; 0.08–0.33 mm wide, short and broad, sub-cylindrical to oval with tapered and usually rounded ends; ventral surface more convex than dorsal; chorion hyaline, but egg colour white to dirty yellow; chorionic surface most often sculptured with elongate, hexagonal reticulations; anterior end simple or provided with lateral flanges, with crown of small projections or anteriorly projecting horns, *etc*. around micropyle (structures purportedly of respiratory function or in eclosion of the larva).

Larva (third-instar) (Fig. 141) differentiated from those of other cyclorrhaphan families by the following combination of characters: body cylindrical, without longer body processes and conspicuous tubercles on posterior segment; cephaloskeleton (Fig. 145) of saprophagous form (including possession of ventral membranous trough enclosing cibarium), *i.e.*, mouthhooks slender (Fig. 145), at most with inconspicuous accessory teeth present; prothoracic spiracle (Fig. 144), positioned laterally or slightly dorsolaterally, not divided into 2 parts, with elongate central axis; posterior spiracular plates (Fig. 143), without hooked or spine-like projections, with more or less evenly rounded margins, plates separated from each other, with 3 slit-like spiracular openings, set at an angle to each other (Fig. 143), these straight or only slightly C-shaped; spiracles set on short or longer fleshy tubular projections, that are widely separated (Fig. 141).

First-instar larva (Fig. 142) 0.6–2.0 mm in length; respiratory system metapneustic, cephaloskeleton very slender (Fig. 147), characterised by mouthhooks anteriorly fused, forming single median tooth; posterior spiracles without definite slit-like spiracular openings but with peristigmatic tuft (Fig. 142). Second-instar larva 1.2–3.8 mm in length, with more spiculae on ventral creeping welts; cephaloskeleton more developed, with 2 mouthhooks (Fig. 146); prothoracic spiracles forming simple, tongue-shaped projections; posterior spiracles with indication of 3 slit-like spiracular openings. Third-instar larva (Fig. 141) 2–6.3 mm in length, 0.5–1.0 mm broad, slender, tapered anteriorly, with somewhat thickened, truncate posterior end; abdominal segments with ventral creeping welts formed of spicules (Fig. 141); cephaloskeleton (Fig. 145), with slender, usually untoothed, paired mouthhooks; intermediate sclerite (Fig. 145), well-developed, separate from basal sclerite; accessory sclerites variable (dental, epistomal and/or ligulate sclerites not always present); basal sclerite (Fig. 145), slender articulating with intermediate sclerite *via* long parastomal bars (Fig. 145); dorsal cornu slender, dorsal bridge markedly separate and usually perforated; ventral cornu larger, often with small window or dorsal apodeme and with conspicuous cibarium (Fig. 145); prothoracic spiracle (Fig. 144), short, fan-shaped, palmate or elongate with numerous (up to 14) lateral spiracular papillae; posterior spiracles (Fig. 141), usually on

Figs 99.20–22. Habitus of Sphaeroceridae: (20) *Ceroptera crispa* (Duda), frontolateral view ♂; (21) *C. nigra* L. Papp, frontolateral view ♂; (22) *Ceropterella mirifica* L. Papp, frontodorsal view ♂. Figs 20, 21 (Papp 2014*b*, figs 97, 99), Fig. 22 (Papp 2017, fig. 25).

sub-cylindrical processes, sometimes sessile (Sphaerocerinae), each with ecdysial scar, three oval to slightly curved slit-like spiracular openings (Fig. 143) and 3–5 sets of branched peristigmatic tufts (Fig. 141).

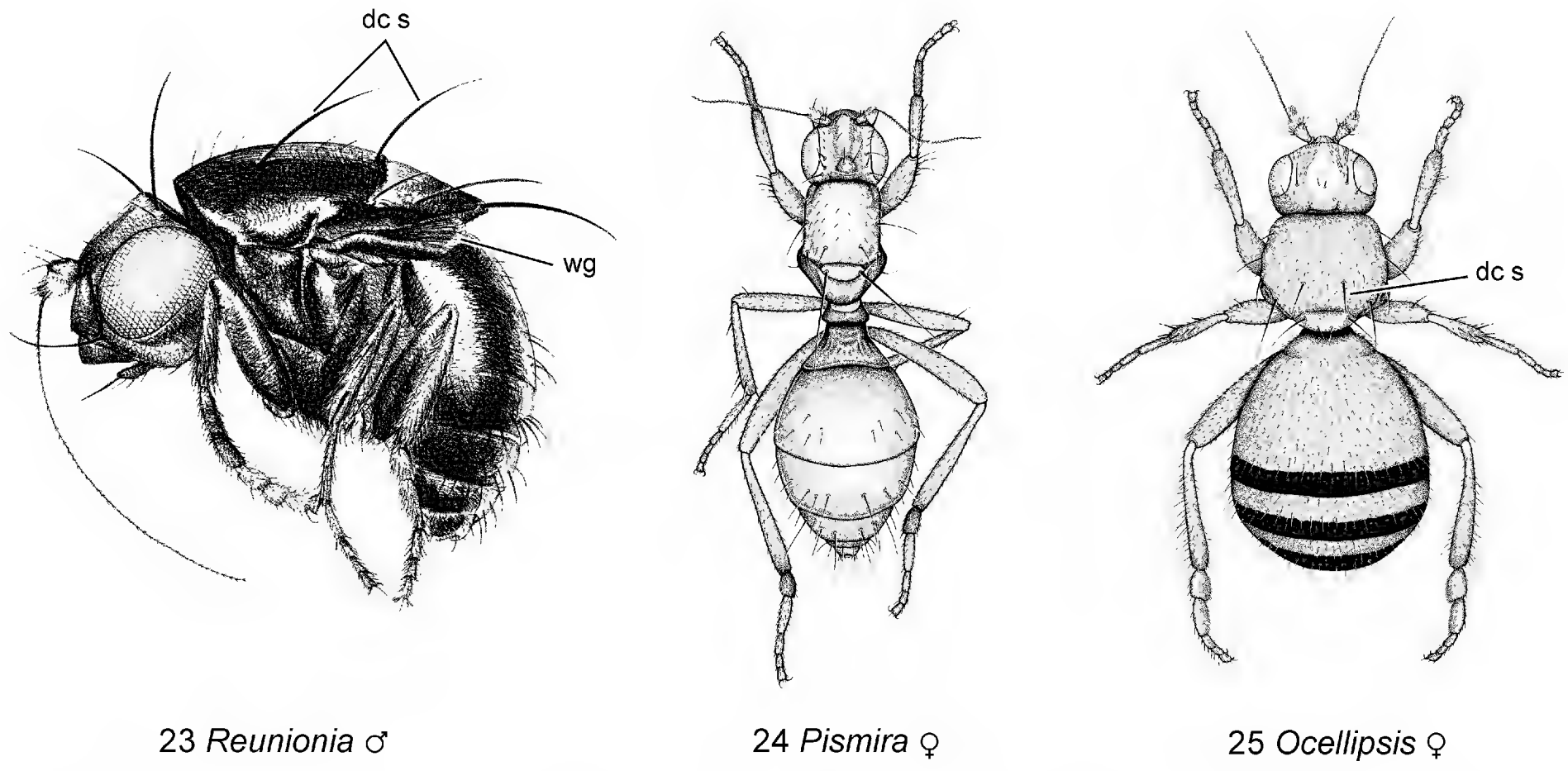
Puparium (Fig. 148) 1.1–4.5 mm in length by 0.3–1.3 mm broad; dirty whitish to brown, barrel-shaped, dorsoventrally slightly compressed, with slightly tapered ends, anteriorly more flattened, with distinctly demarcated thoracic segments; surface transversely finely ribbed or wrinkled; both ends coarsely wrinkled; prothoracic spiracles (Fig. 148) blackish, except for protruding papillae; posterior spiracles (Fig. 148) similar to those of third-instar larva.

Adult Sphaeroceridae are most often confused with the related family Heleomyzidae (see Chapter 98), with some representatives of the subfamily Copromyzinae having similar wing venation and body form. They are easily separated from the Heleomyzidae (and indeed from other Acalyptratae families), however, by the strikingly dilated hind tarsomere 1 (Figs 54–56) and most Heleomyzidae also differ from Copromyzinae by the presence of enlarged spine-like costal setae.

Biology and immature stages

Immature stages of Sphaeroceridae develop in various decaying organic media, with larvae feeding as micro-saprophages on micro-organisms and on liquid components of destructed substances in dung, dead plant material or carrion. Adult flies usually occupy habitats where the breeding media of larvae are accumulated. Species are mostly associated with decayed plant (leaf litter, conifer duff, rotting grass, moss and *Sphagnum*, compost, wood debris, mud, supra-littoral seaweed, fungi, *etc.*) and animal matter (dung, manure, carrion of both vertebrates and invertebrates), in most open and/or woodland terrestrial ecosystems.

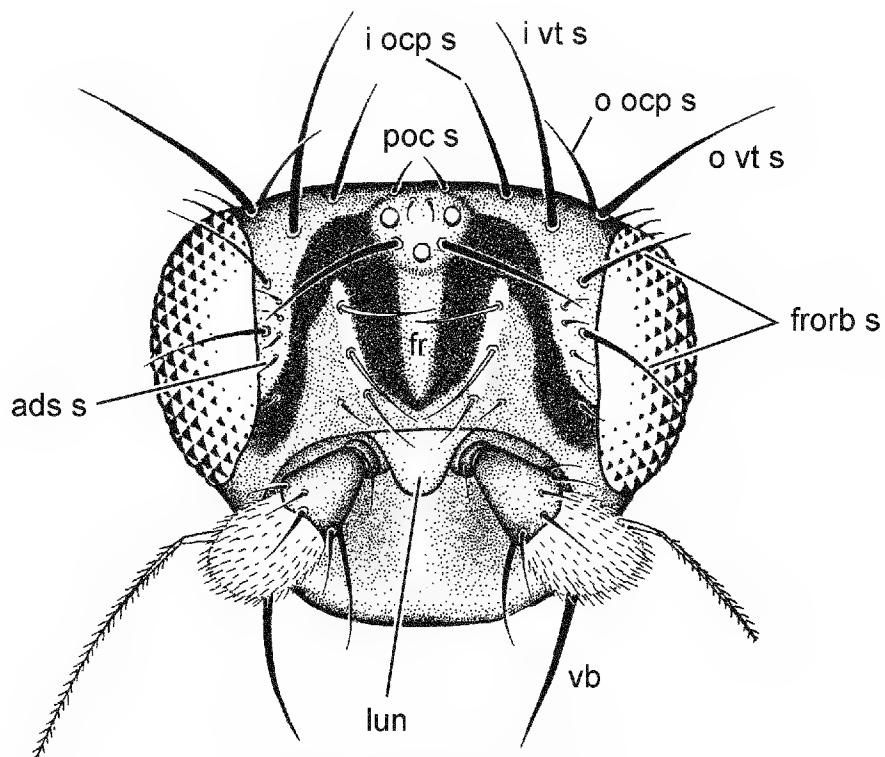
Some species have developed special breeding strategies which enable them to occupy vacant habitat niches, e.g., those utilising organic debris in caves (e.g., Papp & Plachter 1976; Roháček & Košel 1993), burrows of small mammals (e.g., Hackman 1963; Richards 1930; Roháček 2019) and nests of social insects (Richards 1930) or developing in carrion buried by burying beetles (Coleoptera: Silphidae) (Buck 1997). Other species are specialised to utilise decayed plant remnants in bromeliads and similar plants (e.g., Kuwahara & Marshall 2020; Marshall 1983*a*; Yau & Marshall 2018) and larvae of *Archicollinella penteseta* (Richards, 1929) develop in seabird guano and carrion of Cape fur seals, *Arctocephalus pusillus* (Schreber) (Pinnipedia: Otariidae) (Kirk-Spriggs 2007). Enigmatic species of the Neotropical Homalomitrinae are associated with New World army ants (Roháček & Marshall 1998). Adults of *Ceroptera* Macquart and some other species cling to ball-rolling dung beetles (genera *Ateuchus* Weber, *Scarabaeus* L., *etc.*) (Coleoptera: Scarabaeidae) (Marshall 1983*b*; Papp 2014*b*; Sivinski *et al*. 1999) and oviposit into dung balls deposited in their tunnels; minute species of *Opalimosina* Roháček and *Philocoprella* Richards use tunnels of small dung beetles (*Aphodius* Illiger) in cow dung to reach suitable breeding micro-habitat through the encrusted surface. Some species of *Rachispoda* are specialised on mud with high salt content and the majority of *Thoracochaeta* Duda species have larvae that develop in marine algae (kelp) and are halophilous or even halobiont (Marshall & Roháček 2000).



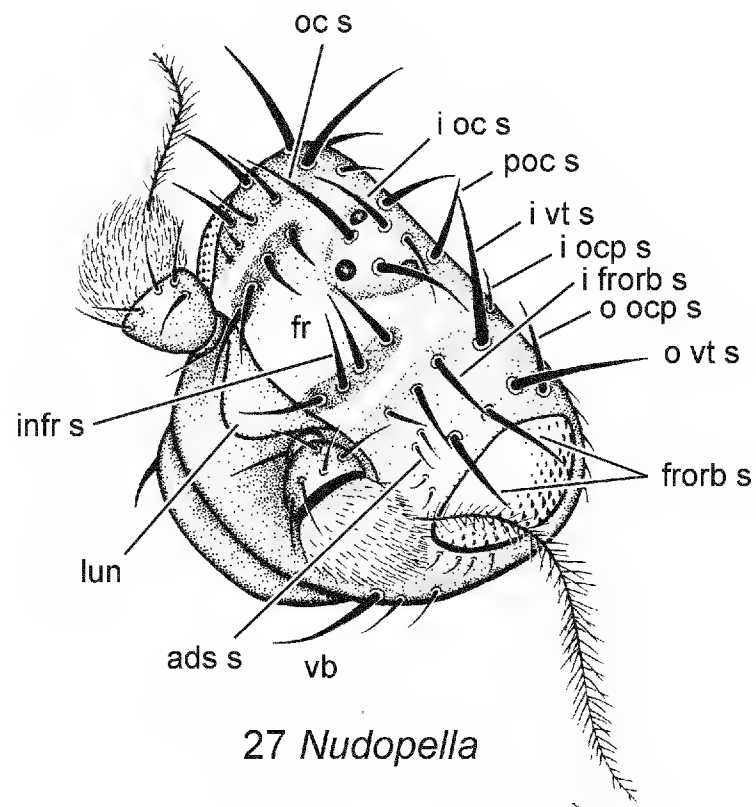
23 *Reunionia* ♂ 24 *Pismira* ♀ 25 *Ocellipsis* ♀

Figs 99.23–25. Habitus of apterous Sphaeroceridae: (23) *Reunionia unica* L. Papp, lateral view ♂; (24) *Pismira uvira* Richards, dorsal view ♀; (25) *Ocellipsis cyclogaster* Richards, dorsal view ♀. Fig. 23 (Papp 1979, fig. 7), Figs 24, 25 (Roháček *et al*. 2001, figs 21, 18, respectively).

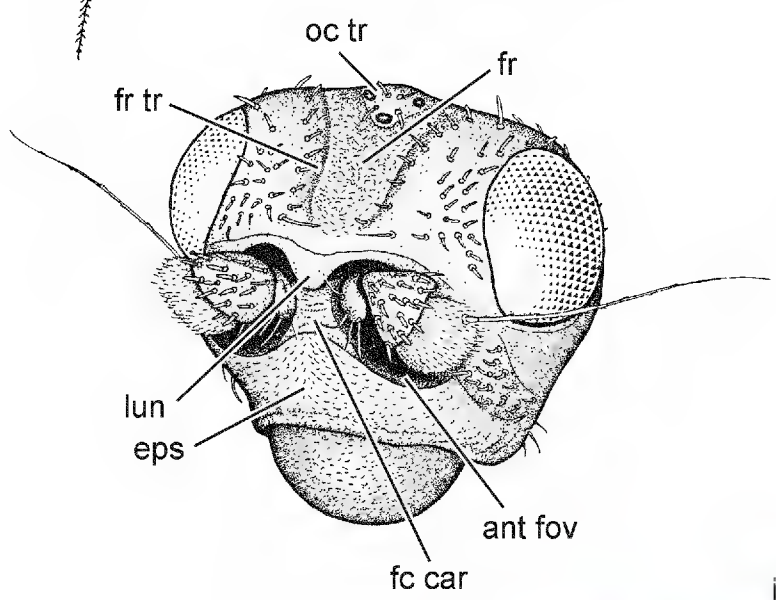
Abbreviations: dc s – dorsocentral seta(e); wg – wing.



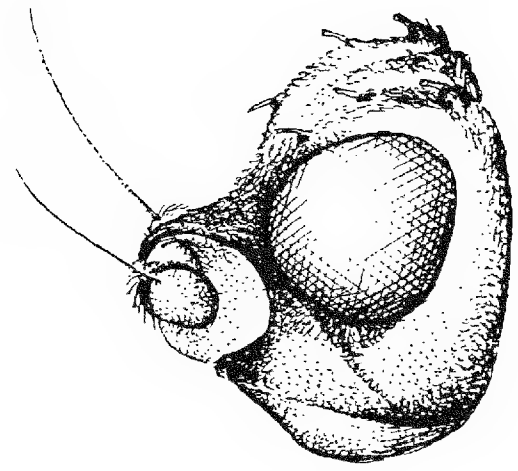
26 *Paralimosina*



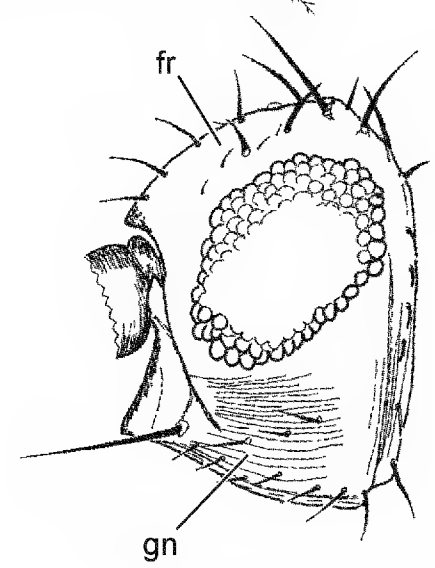
27 *Nudopella*



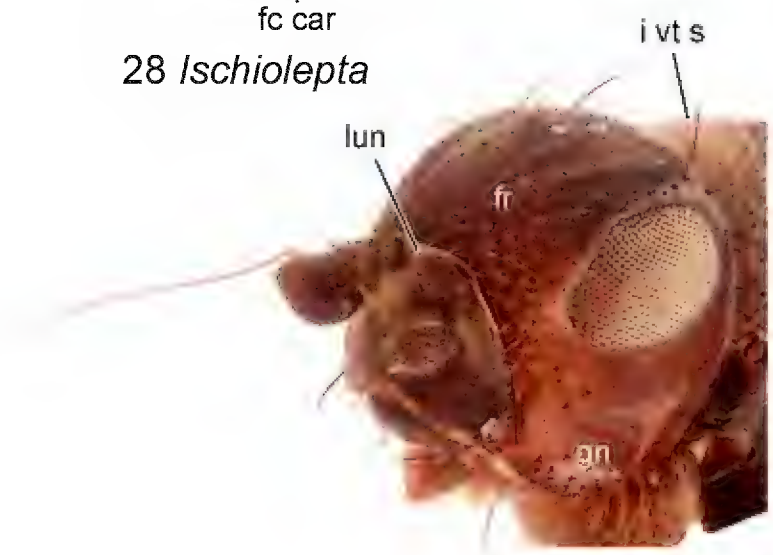
28 *Ischiolepta*



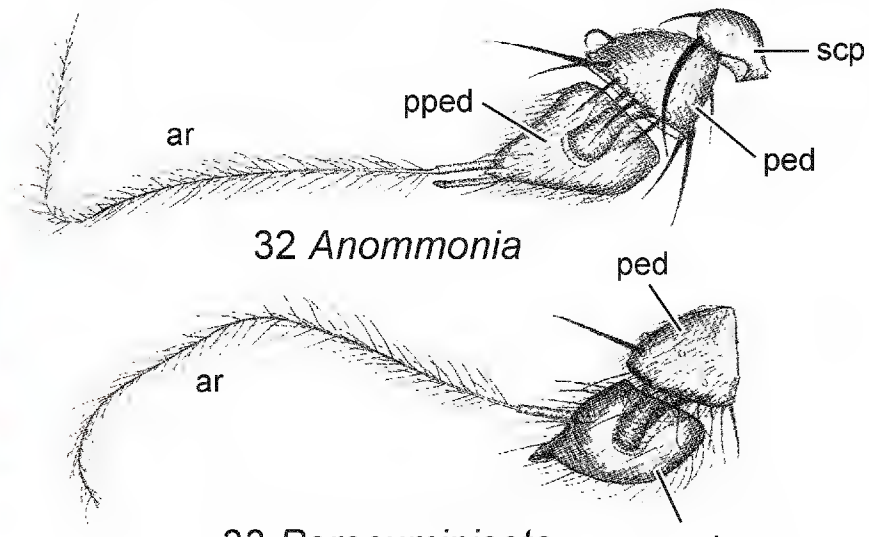
29 *Ischiolepta*



30 *Coproica*



31 *Ceroptera*



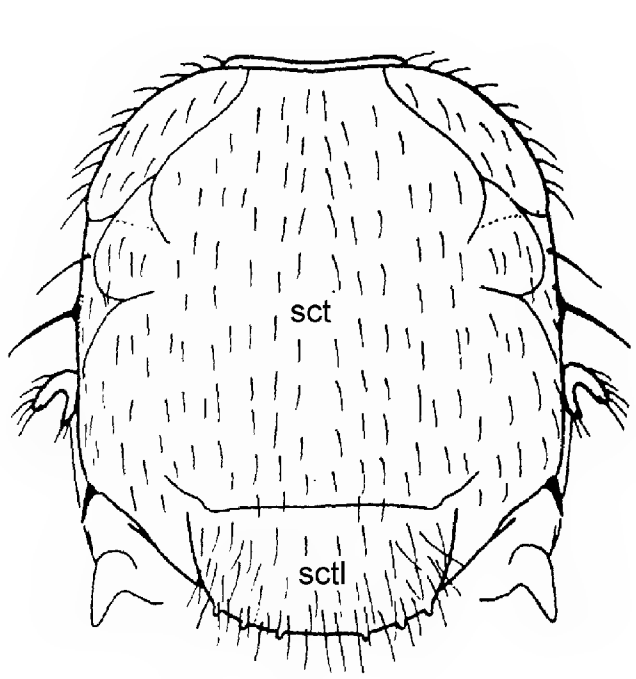
32 *Anommonia*

33 *Paracuminiseta*

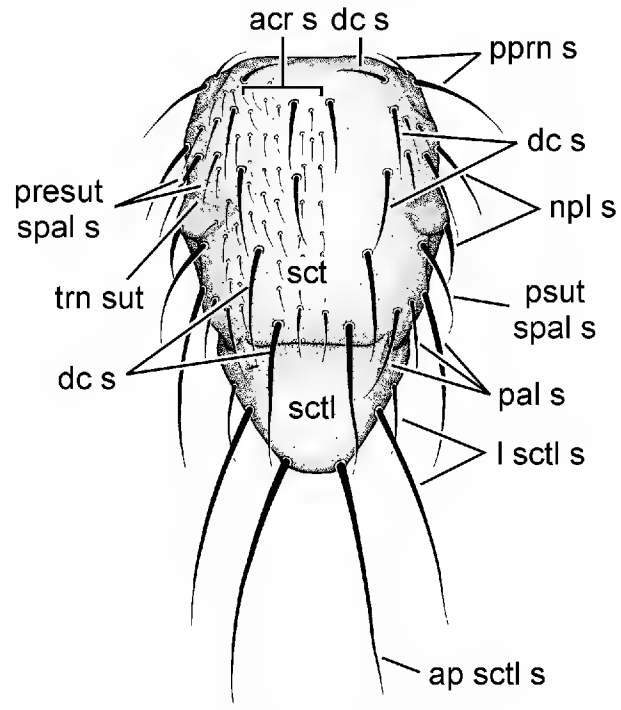
Figs 99.26–33. Heads and antennae of Sphaeroceridae: (26) head of *Paralimosina fucata* (Rondani), frontal view (non-Afrotropical); (27) same, *Nudopella leucoptera* (Haliday), frontodorsal view; (28) same, *Ischiolepta pusilla* (Fallén) (non-Afrotropical); (29) same, *I. vanschuytbroecki* L. Papp, lateral view; (30) same, *Coproica microps* L. Papp; (31) same, *Ceroptera nigra* L. Papp, dorsolateral view; (32) antenna of *Anommonia alopecialis* (Richards), lateral view; (33) same, *Paracuminiseta tetraspinosa* L. Papp. Fig. 26 (Roháček 1983, fig. 333), Fig. 27 (Roháček & Marshall 1986, fig. 2), Fig. 28 (Roháček 1998, fig. 9), Fig. 29 (Papp 1978, fig. 44), Fig. 30 (Papp 2008*a*, fig. 50), Fig. 31 (Papp 2014*b*, fig. 98), Figs 32, 33 (Papp 2008*b*, figs 201, 202).

Abbreviations: ads s – additional seta; ant fov – antennal foveae; ar – arista; eps – epistoma; fc car – facial carina; fr – frons; frorb s – fronto-orbital setae; fr tr – frontal triangle; gn – gena; i frorb s – inner fronto-orbital seta; i oc s – inner ocellar seta; i ocp s – inner occipital seta; i vt s – inner vertical seta; infr s – interfrontal seta; lun – lunule; o ocp s – outer occipital seta; o vt s – outer vertical seta; oc s – ocellar seta; oc tr – ocellar triangle; ped – pedicel; poc s – postocellar seta; pped – postpedicel; scp – scape; vb – vibrissa.

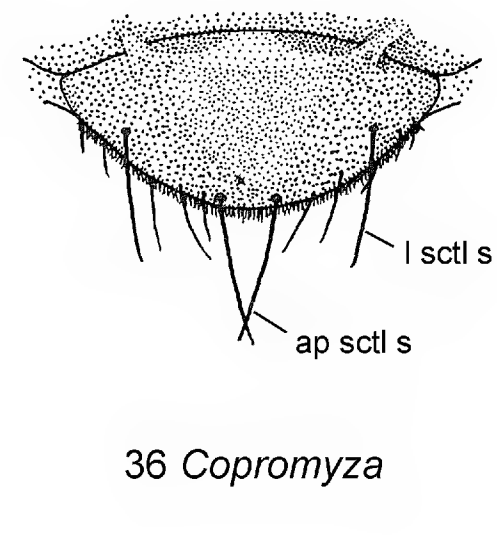
A more comprehensive survey of breeding substrates and habitats of Sphaeroceridae was provided by Ferrar (1987: 345), Marshall (2012: 319), Richards (1930) and Roháček (1982, 1991). The immature stages are undescribed in native Afrotropical taxa, except for the genus *Archicollinella* Duda (Kirk-Spriggs 2007), but they are known for some widespread species also occurring in the region. For more information regarding described larvae and puparia see Ferrar (1987: 345), Okely (1974), Pitkin (1988), Roháček (1982, 1991), Schumann (1962) and Smith (1989: 99).



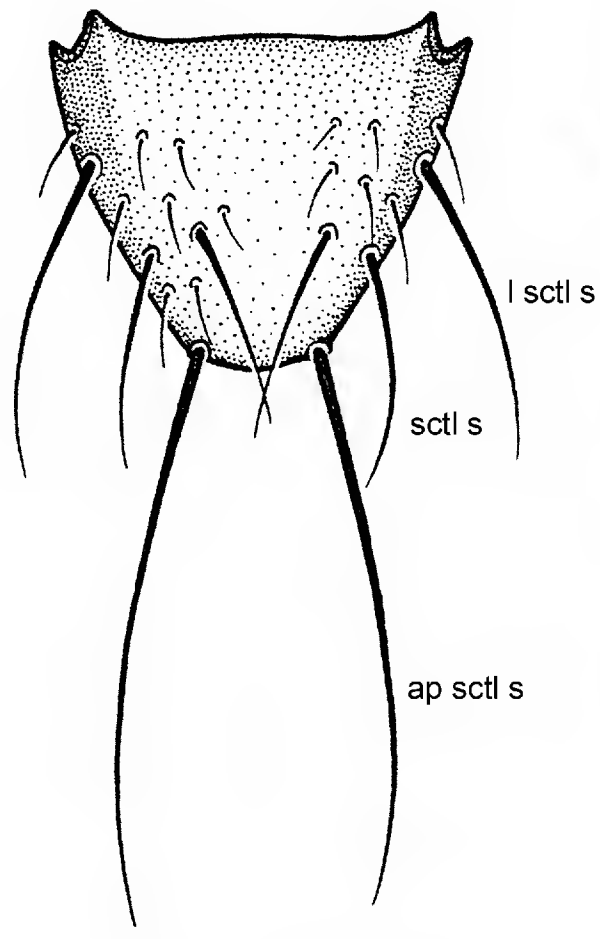
34 *Trichosphaerocera*



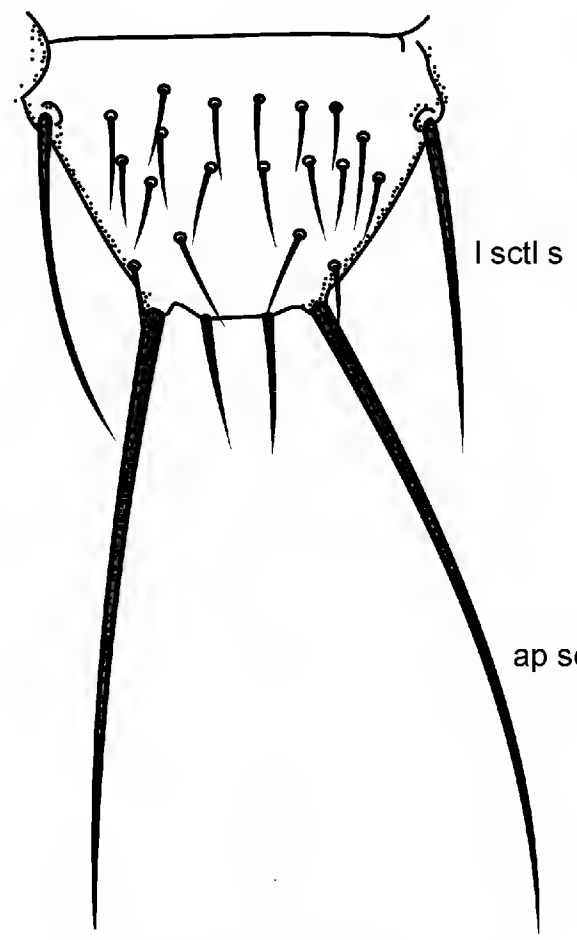
35 *Rachispoda*



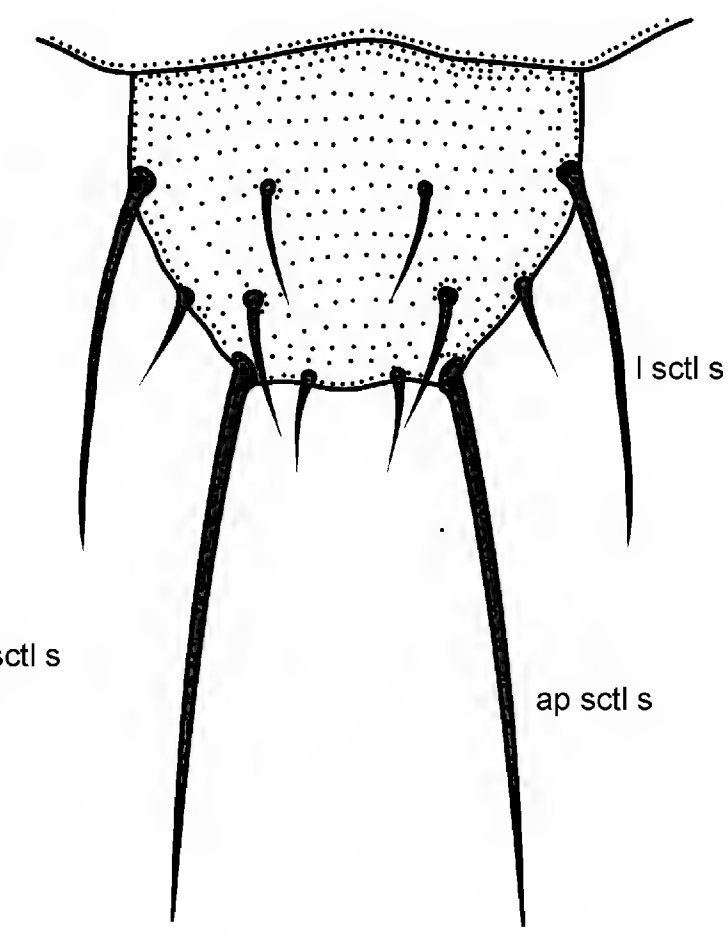
36 *Copromyza*



37 *Rachispoda*



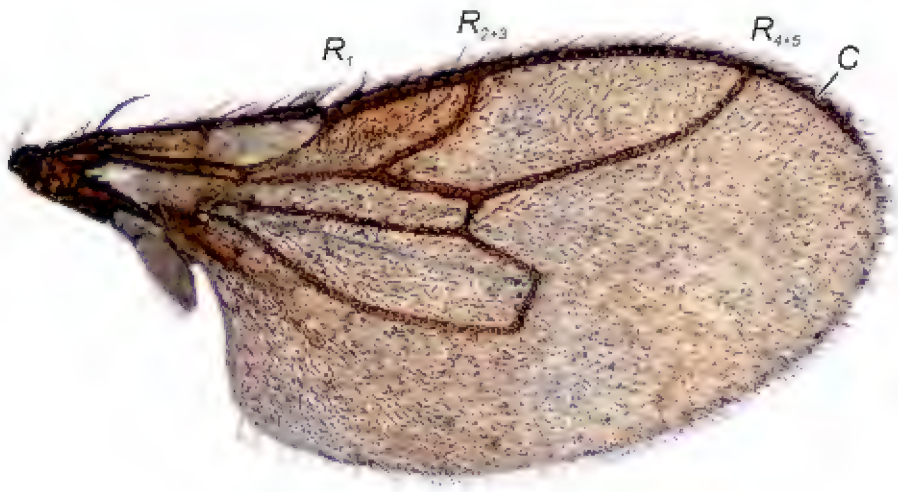
38 *Coproica*



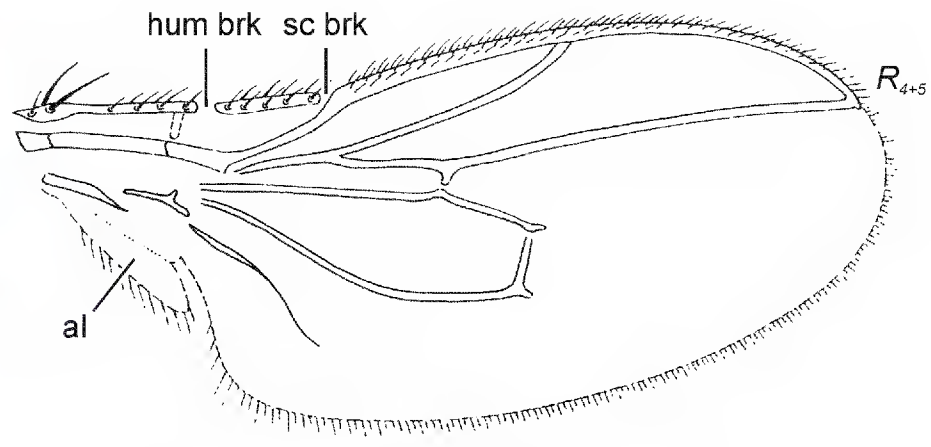
39 *Philocoprella*

Figs 99.34–39. Mesonota and scutella of Sphaeroceridae (dorsal views): (34) mesonotum of *Trichosphaerocera africana* L. Papp; (35) same, *Rachispoda limosa* (Fallén) (non-Afrotropical); (36) scutellum of *Copromyza equina* Fallén (non-Afrotropical); (37) same, *R. fuscipennis* (Haliday); (38) same, *Coproica bispinosa* L. Papp; (39) same, *Philocoprella quadrispinosa* (Laurence) (non-Afrotropical). Fig. 34 (Papp 1978, fig. 37), Fig. 35 (Roháček 1991, fig. 24), Figs 36, 39 (Papp 1973, figs 12H, 12F, respectively), Fig. 37 (Roháček 1991, fig. 28), Fig. 38 (Papp 2008*a*, fig. 84).

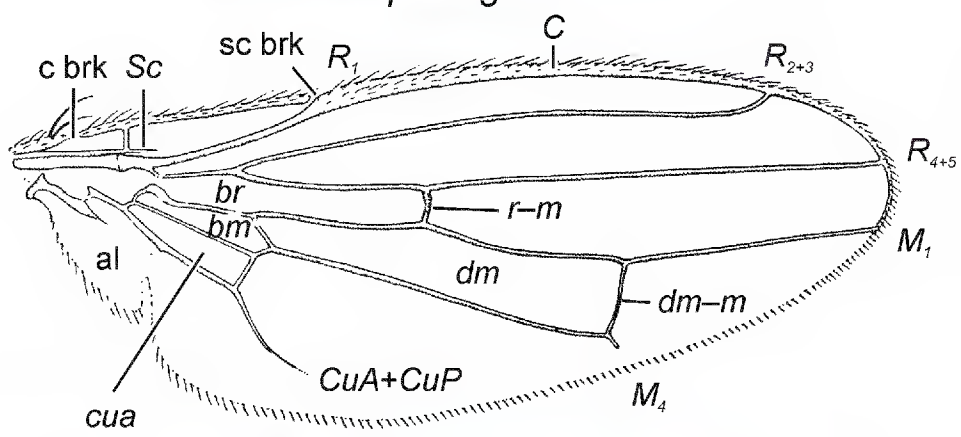
Abbreviations: acr s – acrostichal setae; ap sctl s – apical scutellar seta; dc s – dorsocentral setae; l sctl s – lateral scutellar seta(e); npl s – notopleural setae; pal s – postalar seta; pprn s – postpronotal setae; presut spal s – presutural supra-alar setae; psut spal s – postsutural supra-alar seta; sct – scutum; sctl – scutellum; sctl s – scutellar seta; trn sut – transverse suture.



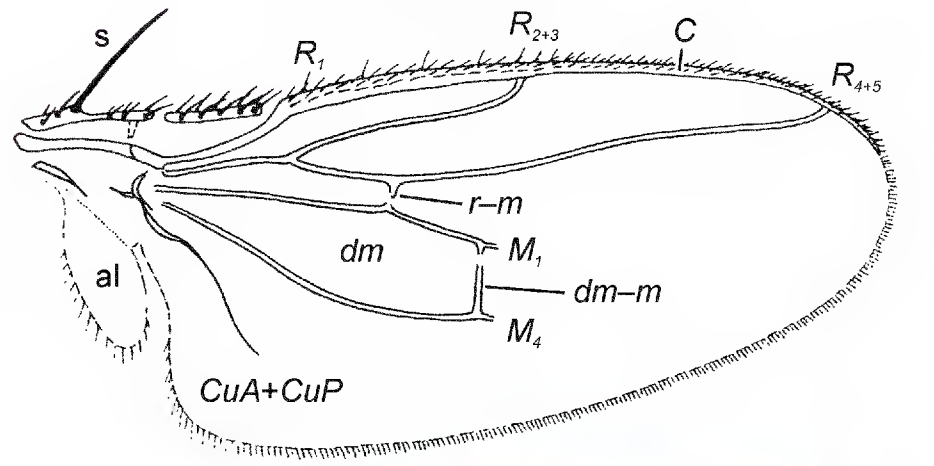
40 *Afropterogramma*



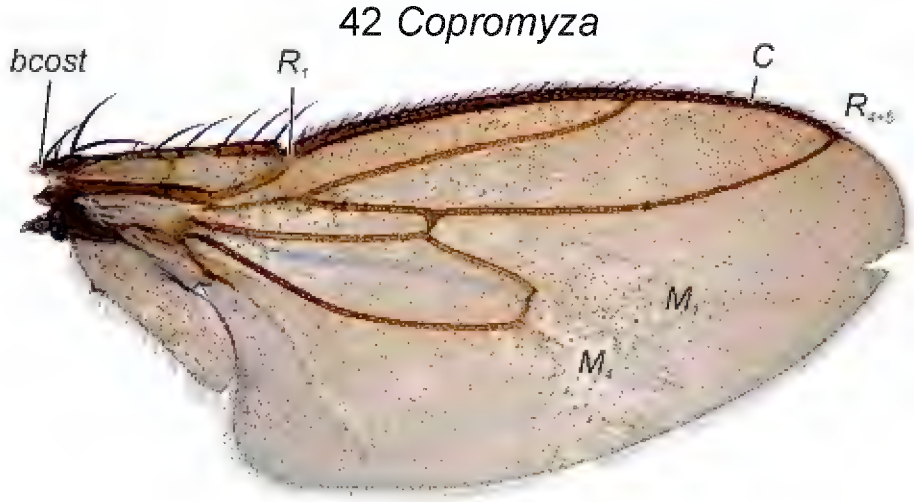
41 *Bifronsina*



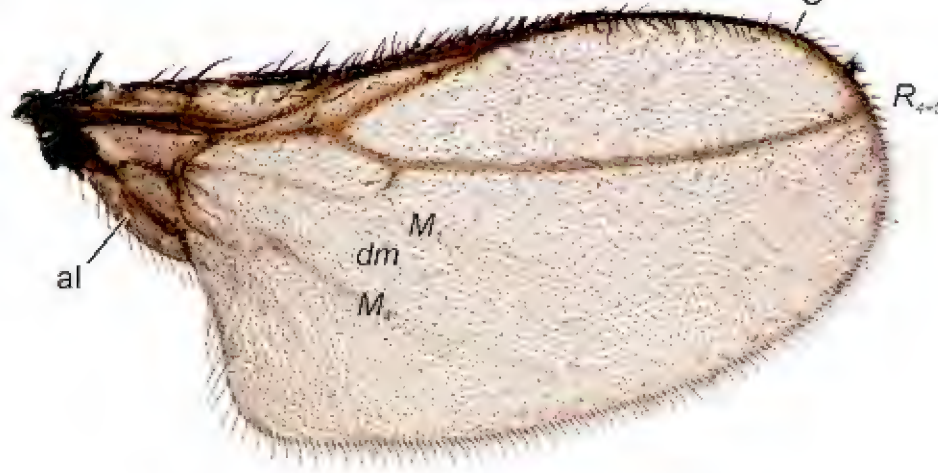
42 *Copromyza*



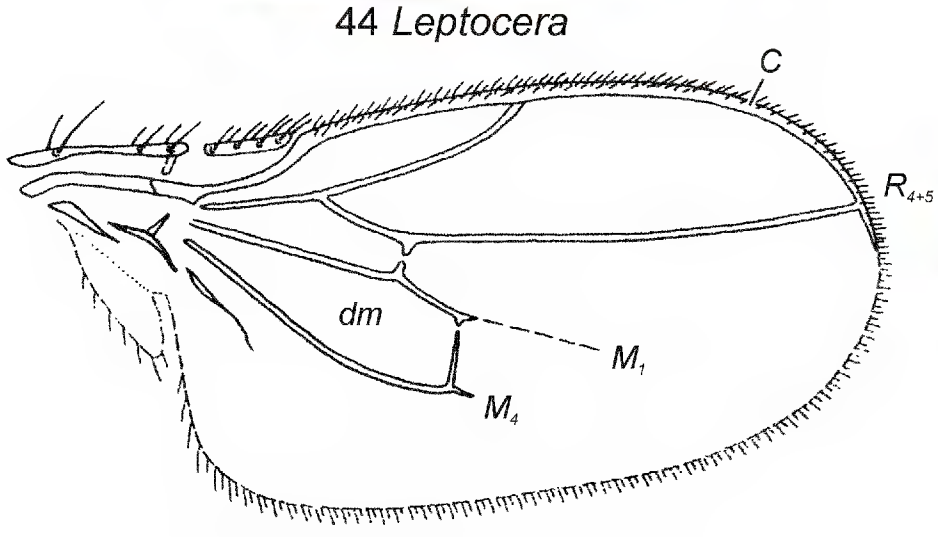
43 *Gonioneura*



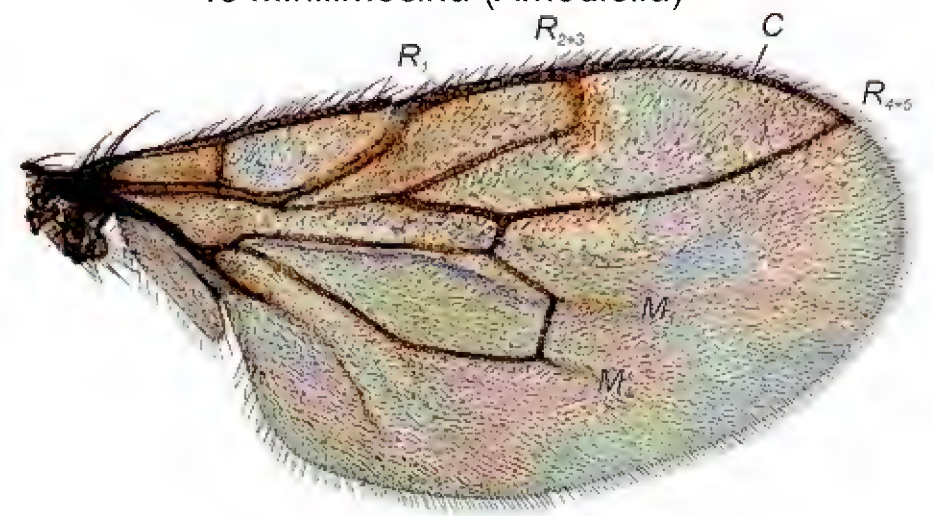
44 *Leptocera*



45 *Minilimosina* (*Amediella*)



46 *Minilimosina* (*Allolimosina*)



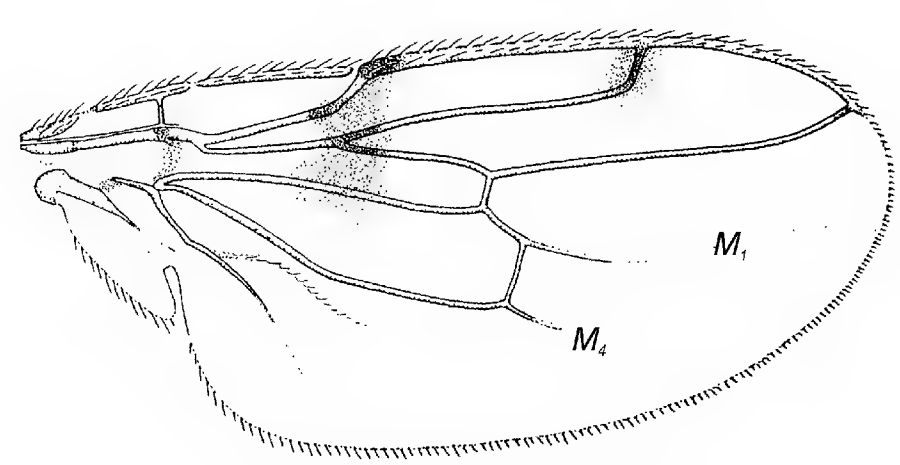
47 *Parapoecilosomella*

Figs 99.40–47. Wings of Sphaeroceridae (dorsal views): (40) *Afropterogramma minor* L. Papp; (41) *Bifronsina bifrons* (Stenhammar); (42) *Copromyza equina* Fallén (non-Afrotropical); (43) *Gonioneura spinipennis* (Haliday) (non-Afrotropical); (44) *Leptocera kovacsi* Duda; (45) *Minilimosina* (*Amediella*) *endrodyi* L. Papp; (46) *M.* (*Allolimosina*) *albinervis* (Duda) (non-Afrotropical); (47) *Parapoecilosomella lusingana* (Vanschuytbroeck). Figs 40, 44, 45, 47 (photographs Z. Soltész), Figs 41, 43 (Roháček 1985, figs 695, 1089), Figs 42, 46 (Roháček 1998, figs 21, 29).

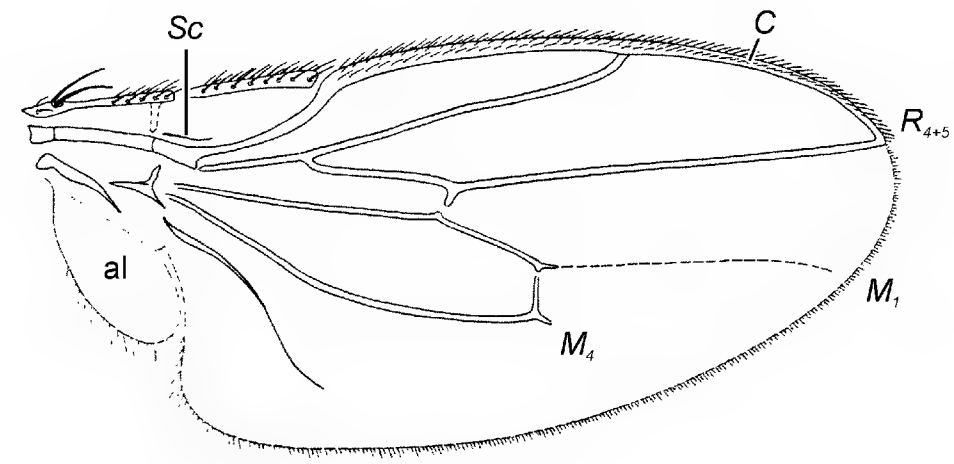
Abbreviations: al – alula; *bm* – basal medial cell; *bcost* – basicosta; *br* – basal radial cell; *C* – costal vein; c brk – costagial break; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *dm* – discal medial cell; *dm–m* – discal medial crossvein; hum brk – humeral break; M_1 – first branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; s – seta; *Sc* – subcostal vein; sc brk – subcostal break.

The family includes many species exhibiting wing polymorphism, with apterous, brachypterous and stenopterous species, mostly adapted to edaphic, subterranean, high mountain or island habitats, as studied by Richards (1951*a*, *b*, 1953, 1954, 1955, 1957, 1959, 1960*a*, *b*, 1963, 1965, 1968*a*, *b*).

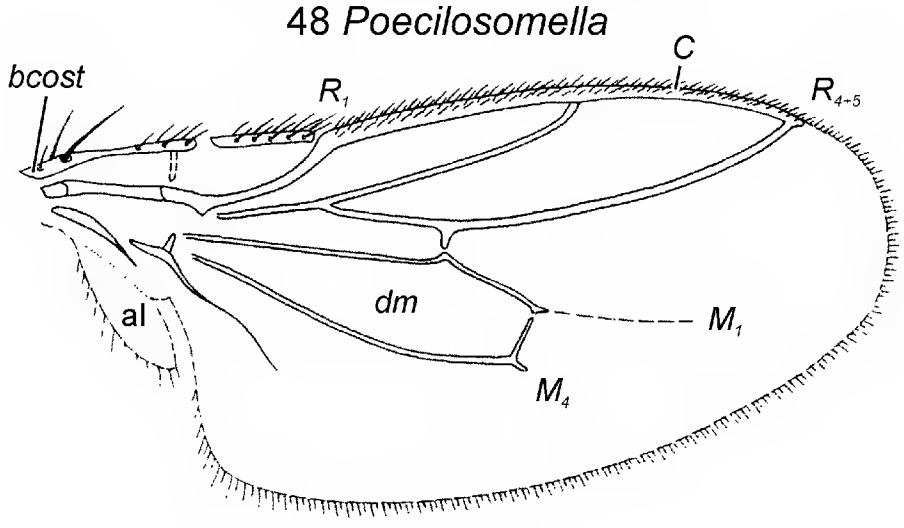
The duration of the life cycle is extremely variable in Sphaeroceridae and may be very short in certain species developing at higher temperatures, e.g., five days in some *Coproica* Rondani species (Hafez 1939), but long in cold-adapted species (e.g., in caves or arctic environment up to 1 year). Thus, many species are multivoltine, but the number of generations may be drastically reduced at higher elevations and/or latitudes. The puparium is usually the overwintering stage, although other species are also known to occur as adults or larvae in winter. A parthenogenetic reproduction (probably conditioned



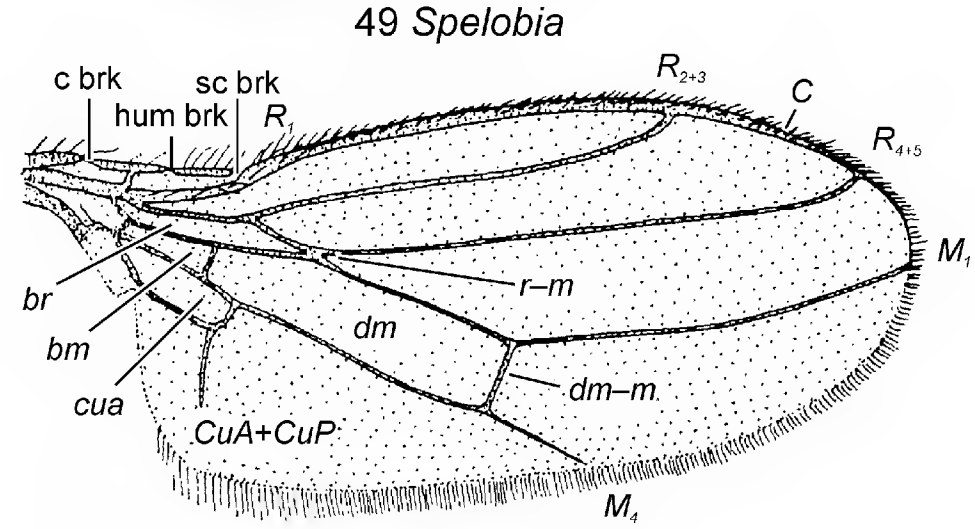
48 *Poecilosomella*



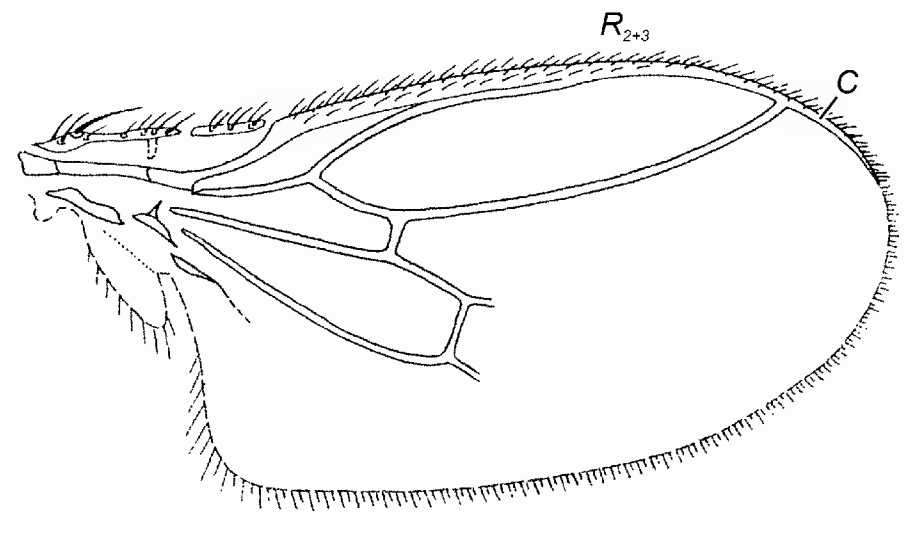
49 *Spelobia*



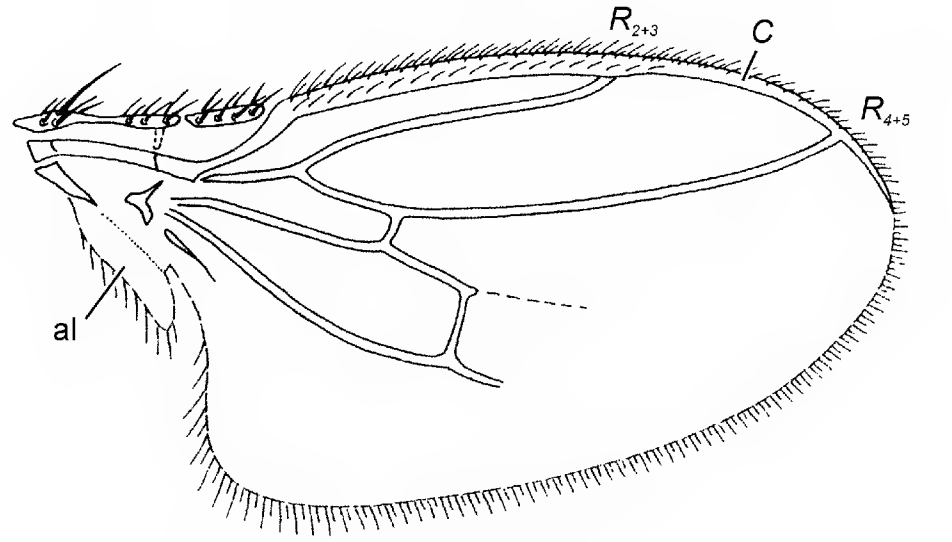
50 *Spinilimosina*



51 *Trichosphaerocera*



52 *Trachyopella* (*Insulomyia*)



53 *Nudopella*

Figs 99.48–53. Wings of Sphaeroceridae (dorsal views): (48) *Poecilosomella angulata* (Thomson); (49) *Spelobia clunipes* (Meigen) (non-Afrotropical); (50) *Spinilimosina brevicostata* (Duda); (51) *Trichosphaerocera africana* L. Papp; (52) *Trachyopella* (*Insulomyia*) *artivena* Roháček (non-Afrotropical); (53) *Nudopella leucoptera* (Haliday) (non-Afrotropical). Fig. 48 (Roháček 1998, fig. 25), Fig. 49 (Roháček 1983, fig. 439), Fig. 50 (Roháček 1985, fig. 807), Fig. 51 (Papp 1978, fig. 36), Figs 52, 53 (Roháček & Marshall 1986, figs 13, 9, respectively).

Abbreviations: al – alula; *bm* – basal medial cell; *bcost* – basicosta; *br* – basal radial cell; *C* – costal vein; c brk – costagial break; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *dm* – discal medial cell; *dm–m* – discal medial crossvein; hum brk – humeral break; M_1 – first branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; sc brk – subcostal break; *Sc* – subcostal vein.

geographically) has been confirmed in three Palaearctic species: *Copromyza neglecta* (Malloch, 1913), *Pullimosina pullula* (Zetterstedt, 1847) and *Spelobia parapusio* (Dahl, 1909) (Okely 1974; Roháček 1989), but it is probable that such cases also occur in the Afrotropics.

Economic significance

Although Sphaeroceridae are among the most common and omnipresent flies, they are usually not of direct economic or medical importance (Cogan 1973: 281). Some species are at least partly synanthropic and may reach nuisance levels when occurring in large numbers indoors (Fredeen & Taylor 1964; Marshall & Richards 1987: 994; Mihara *et al*. 1983*a*, *b*; Nicoli *et al*. 1962; Roháček 1991). In Europe, certain species (*Coproica* spp., *Pullimosina heteroneura* (Haliday, 1836) and *Spelobia parapusio*) are occasionally noted as pests in mushroom cultures, either by direct larval feeding or by their involvement in dissemination of nematodes (Haglund & Milne 1973). *Thoracochaeta johnsoni* (Spuler, 1925) was recorded as a pest in oyster-processing plants in Japan (Marshall & Richards 1987: 994). Some species, primarily *Coproica* species, cause problems in virus-free egg production, as adults can access confinement areas and thus negate exemption. A case of human intestinal myiasis caused by *Poecilosomella angulata* (Thomson, 1869) was described by Micks & McKibbon (1956). While the direct economic importance of Sphaeroceridae is rather small, they appear to play a significant positive role in the decomposing process of organic matter, contributing to nutrient cycling. Owing to their ability to rapidly breed under suitable conditions, Sphaeroceridae form an important component of insect communities in habitats with cumulated decaying media, *e.g.*, dung on pastures and manure heaps (Papp 1974*a*, *b*, 1976, 1985, 1992, 1993, 2007), salt lake shore mud (Papp & Izsák 2008), seashore wrack and woodland leaf litter and may thus have an indirect impact on soil fertility.

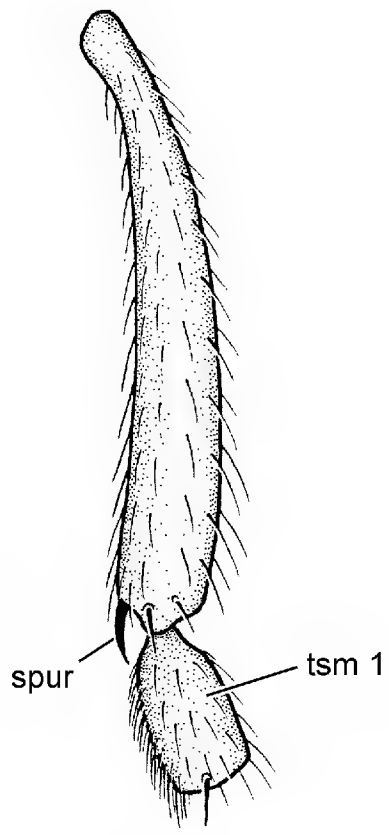
Classification

McAlpine (1989: 1479) postulated that the Sphaeroceridae belonged, together with the families Chyromyidae, Heleomyzidae (*sensu* McAlpine 1985, *i.e.*, including Rhinotoridae and Trixoscelididae) and (?) Mormotomyiidae, in the superfamily Sphaeroceroidea (= Heleomyzoidea). Although this grouping was supported by only one synapomorphy (the enlarged and complex distiphallus), there are several other features shared by Chyromyidae, Sphaeroceridae and certain tribes of Heleomyzidae. Chyromyidae were suggested to be the putative sister-group of Sphaeroceridae by McAlpine (1989: 1483), but it is plausible that sister-groups of both these families will be found among different tribes of the (paraphyletic) family Heleomyzidae (*sensu* McAlpine 1985) as and when the postabdominal structures are better known. A further split of the Heleomyzidae into several families is, therefore, to be expected in the future. McAlpine (2007) even suggested that Sphaeroceridae should be reduced to a subfamily within his newly defined "Heteromyzidae" (also including the Heleomyzidae as currently recognised). This action would lead to reduction of the subfamilies of Sphaeroceridae (see below) to tribes. Marshall *et al*. (2011) recognised that the current concept of Heleomyzidae is obviously paraphyletic regarding the Sphaeroceridae, but suggested that combining these two large and widely recognised families at this time would serve no useful purpose and would destabilise sphaerocerid nomenclature. The close relationship of Sphaeroceridae to Heleomyzidae has recently also been supported by phylotranscriptomic hypothesis by Bayless *et al*. (2021).

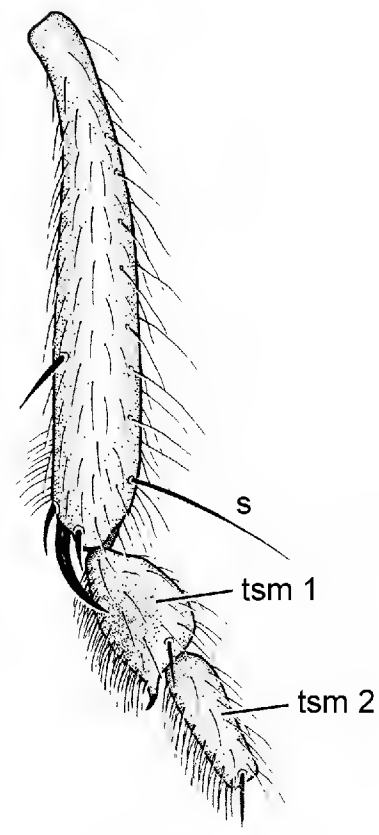
Higher classification of the Sphaeroceridae is well founded as regards subfamilies (see below), but the relationships of some enigmatic or poorly known extra-Holarctic genera, such as *Pycnopota* Bezzi (Kits *et al*. 2013) remain unclear and their placement is uncertain. Six subfamilies are recognised, three of which are restricted to the Neotropical Region: the speciose Archiborborinae (as redefined by Kits *et al*. 2013) and small Tucminae (Marshall 1996) and Homalomitrinae (Roháček & Marshall 1998), each comprise a few aberrant genera. In the Afrotropical fauna, only three other subfamilies (all widespread in all zoogeographical regions, except for Antarctica) are recognised: the Copromyzinae, representatives of which retain more plesiomorphic features and most closely resemble Heleomyzidae; the Sphaerocerinae, a morphologically specialised sister-group to Copromyzinae (Kits *et al*. 2013); and the Limosininae, which differ most from the hypothetical ancestor and are (together with the Homalomitrinae) probably an early branching offspring of the common ancestor of all other earlier mentioned subfamilies (Roháček & Marshall 1998).

The first studies dealing with Sphaeroceridae from tropical Africa were those by Adams (1905), Becker (1909, 1910*a*, *b*), Bezzi (1908), Collin (1912), Macquart (1835), Schmitz (1917) and Villeneuve (1916), but the first significant works on Afrotropical Sphaeroceridae were those of Duda (1920, 1923, 1925, 1926). From 1938–1968, O.W. Richards published 18 papers on Afrotropical Sphaeroceridae, particularly dealing with the apterous and short-winged forms (Richards 1938, 1939, 1950, 1951*a*, *b*, 1953, 1954, 1955, 1957, 1959, 1960*a*, *b*, 1963, 1965, 1966, 1968*a*, *b*, *c*). He described numerous genera for reduced-winged forms, but retained the "traditional" huge genera, particularly *Leptocera*, undivided. Séguy (1933, 1952, 1955) examined Sphaeroceridae from some parts of the region and described a few genera and species. Later, Vanschuytbroeck (1945, 1948, 1950*a*, *b*, 1951*a*, *b*, 1959*a*, *b*, 1962, 1970, 1977) studied Afrotropical Sphaeroceridae and described new species in more than 10 papers, particularly from Central Africa, but his studies contributed little to taxonomic knowledge, due to numerous inaccuracies and misinterpretations. Hackman (1965, 1967) published two important publications on Malagasy and South African sphaerocerids, but otherwise the new information on the fully winged Afrotropical sphaerocerids remained sporadic for some 50 years. As a result, Hackman's (1969) summary of the zoogeography of world Sphaeroceridae was somewhat premature, at least as regards the Afrotropical fauna, but he elevated several of Duda's and Richards' fully winged subgenera to generic level and began the re-classification of the extremely large collective genus *Leptocera* (= *Limosina*) of previous authors.

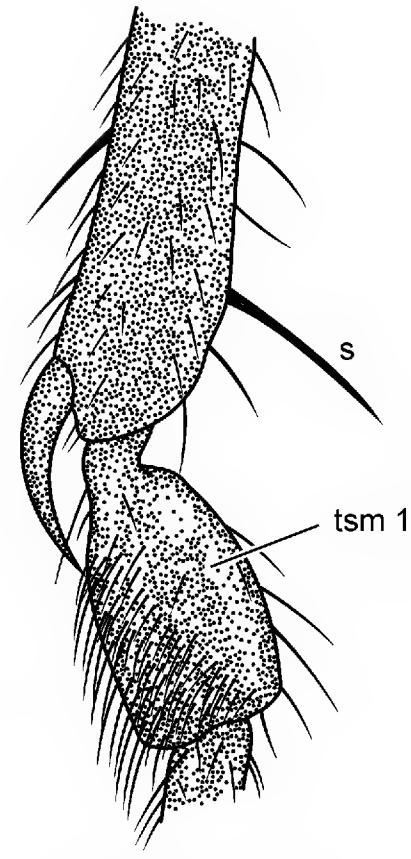
Roháček's (1982, 1983, 1985) monograph on European Limosininae, with its "re-classification of the previous genus *Limosina* Macquart" had a more fundamental influence on the classification of all Limosininae, including those species occurring in the continental Afrotropics. Other important works with a modern taxonomical view and with good illustrations



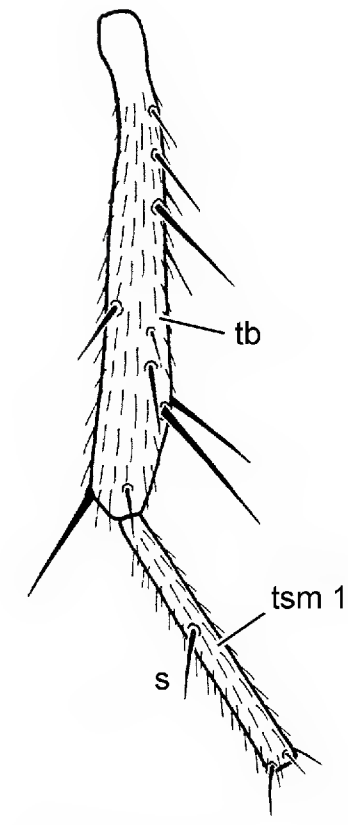
54 *Ceroptera*



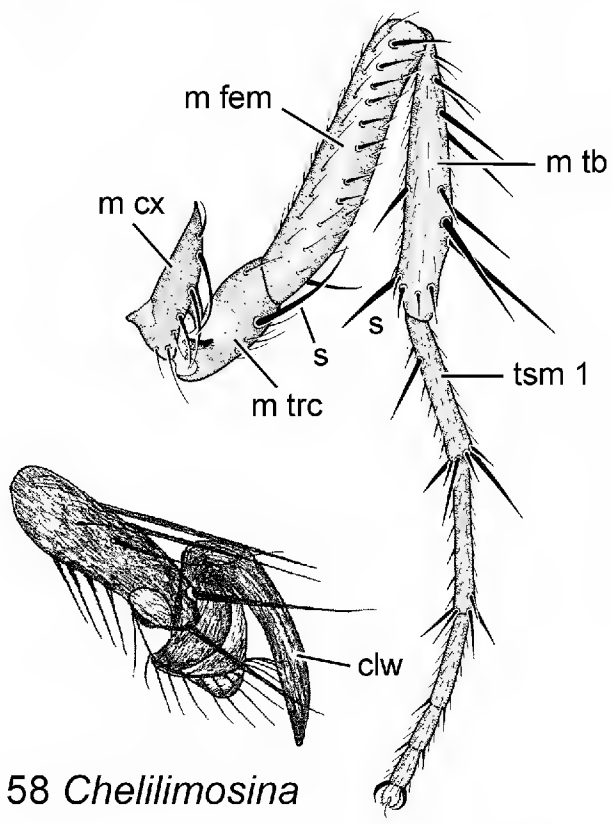
55 *Crumomyia*



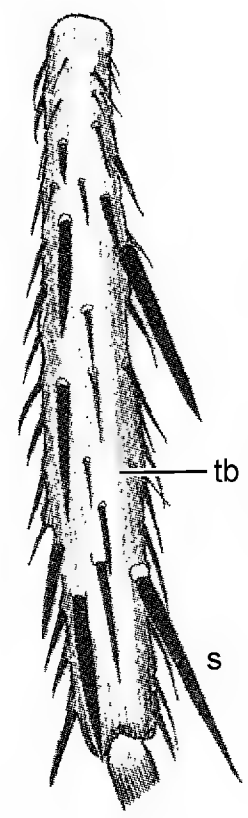
56 *Norrbomia*



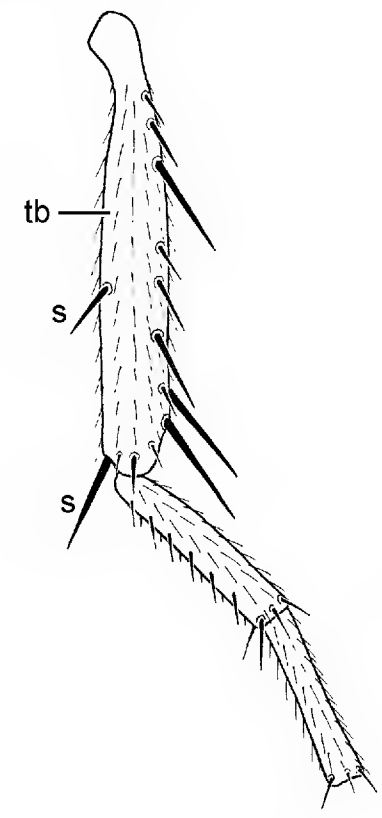
57 *Chaetopodella* (*Chaetopodella*)



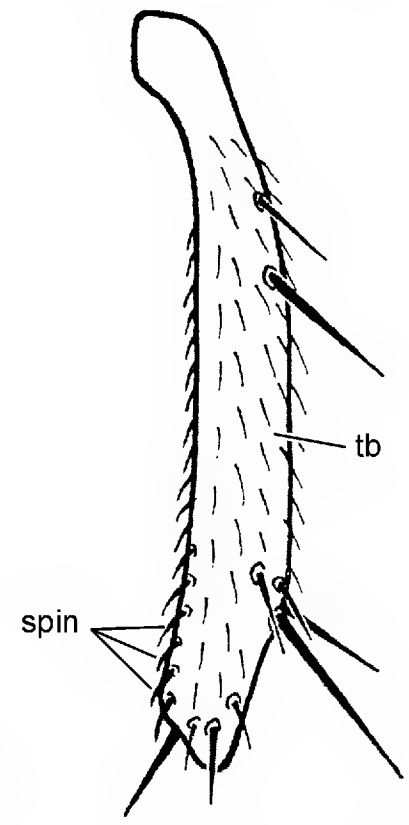
58 *Chelilimosina*



59 *Rachispoda*



60 *Eximilimosina*



61 *Spelobia*

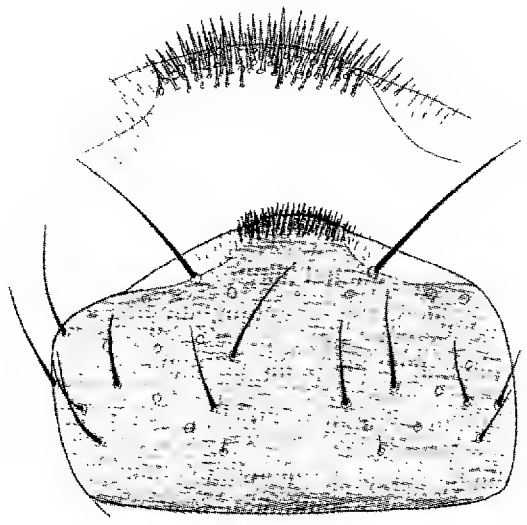
62 *Eulimosina*

Figs 99.54–62. Leg features of Sphaeroceridae: (54) hind tibia and tarsomere 1 of *Ceroptera algira* (Villeneuve), anterior view ♂ (non-Afrotropical); (55) same, hind tibia and tarsomeres 1 and 2 of *Crumomyia nigra* (Meigen) ♂ (non-Afrotropical); (56) apex of hind tibia and tarsomere 1 of *Norrbomia sordida* (Zetterstedt), anterior view ♂ (non-Afrotropical); (57) mid tibia and tarsomere 1 of *Chaetopodella* (*Chaetopodella*) *scutellaris* (Haliday), anterior view ♀ (non-Afrotropical); (58) fore tarsomere 5 of *Chelilimosina baloghi* L. Papp, lateral view ♂; (59) mid leg of *Rachispoda limosa* (Fallén), anterior view ♂ (non-Afrotropical); (60) mid tibia of *Eximilimosina thailandica* L. Papp, dorsal view ♂ (non-Afrotropical); (61) mid tibia and tarsomeres 1 and 2 of *Spelobia clunipes* (Meigen), anterior view ♂ (non-Afrotropical); (62) mid tibia of *Eulimosina ochripes* (Meigen), anterior view ♂ (non-Afrotropical). Figs 54, 55 (Roháček 1998, figs 56, 61), Fig. 56 (Papp 1973, fig. 11A), Fig. 57 (Roháček 1985, fig. 820), Fig. 58 (Papp 2014*a*, fig. 49 © Magnolia Press), Fig. 59 (Roháček 1991, fig. 32), Fig. 60 (Papp 2008*b*, fig. 49), Figs 61, 62 (Roháček 1983, figs 453, 422, respectively).

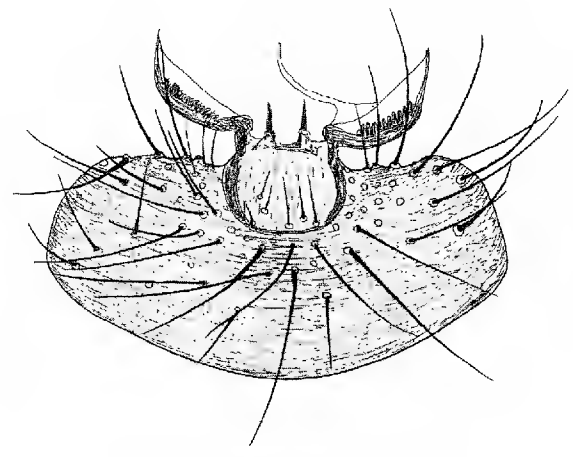
Abbreviations: clw – claw; m cx – mid coxa; m fem – mid femur; m tb – mid tibia; m trc – mid trochanter; s – seta; spin – spinules; spur – spur; tb – tibia; tsm – tarsomere.

include revisions and monographs by H.-Y. Han, K.C. Kim, S.A. Marshall, A.L. Norrbom, L. Papp and J. Roháček, published from the end of the 1970s (for references see "Synopsis of fauna" section below). The supra-specific classification of Sphaeroceridae is under rapid development, particularly within the Limosininae, where substantial advances have been made over the past 40 years (e.g., Hayashi 2006; Kim 1972; Kits & Marshall 2011, 2013, 2015; Luk & Marshall 2014; Marshall 1987, 1995, 1997, 1998, 2000*a*, *b*, 2001, 2013, 2014; Marshall & Buck 2010: 1165; Marshall & Cui 2005; Marshall & Dong 2008; Marshall & Roháček 2003; Marshall & Smith 1992, 1993, 1995; Marshall & Yau 2014, 2019; Marshall *et al*. 2007, 2014, 2015; Papp 1972, 1977, 1979, 1981, 1988, 2004*a*, *b*, 2008*b*, 2010, 2012*a*, *b*, 2013, 2014*a*; 2016; Richards 1973; Roháček 1982, 1983, 1985; Roháček & Marshall 1982, 1986: 7, 1998, 2017; Roháček & Papp 1988; Smith & Marshall 2004; Yau & Marshall 2018). Although only minor additions and alterations of the system of genera are probable in the Holarctic fauna, much progress is expected in research on the supra-specific classification of Sphaeroceridae in other parts of the world, including the Afrotropical Region, as evidenced by numerous new genera having been recently described from the region by Papp (2008*b*, 2014*a*).

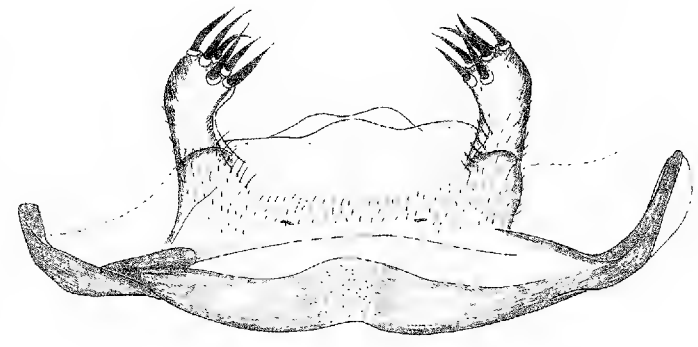
Afrotropical species of the family were first catalogued by Richards (1980: 614), although this treatment is now out of date, considering the numerous new taxa subsequently added. Only the "World catalog of the family Sphaeroceridae" (Roháček *et al*. 2001) and its update covering the years 2001–2010 by Marshall *et al*. (2011) essentially improved the



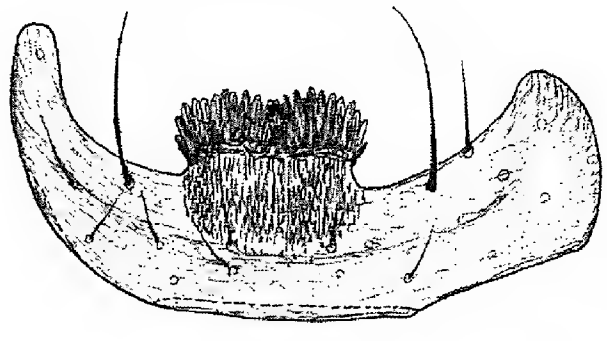
63 *Piliterga* ♂



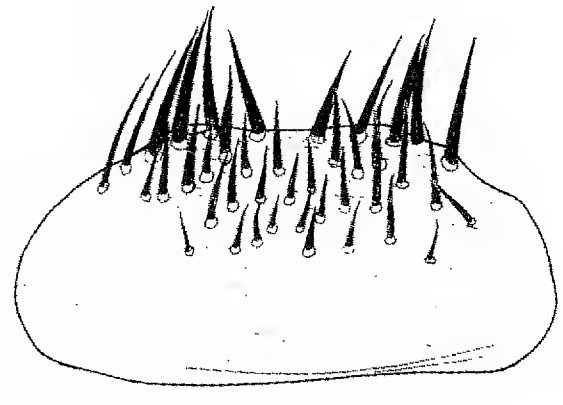
64 *Mislocatus* ♂



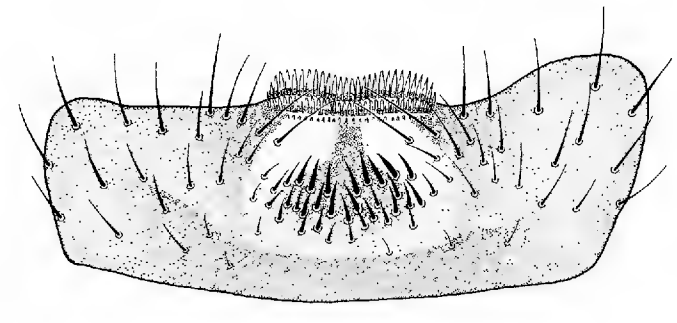
65 *Chaetopodella* (*Chaetopodella*) ♂



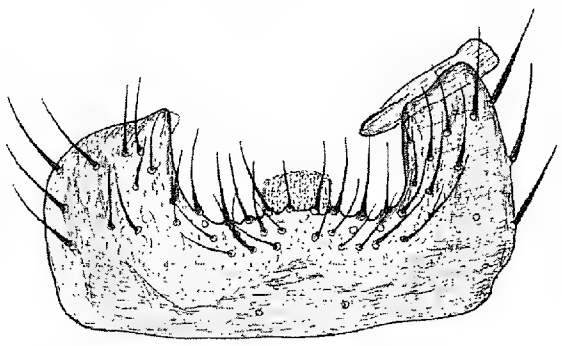
66 *Permixtolimosina* ♂



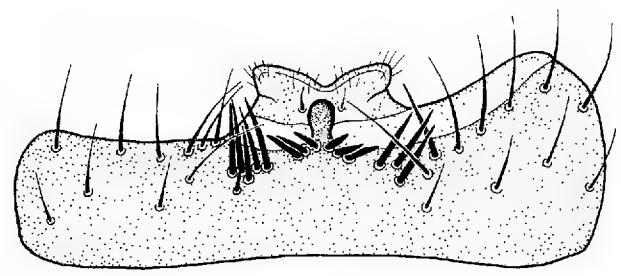
67 *Acuminiseta* ♂



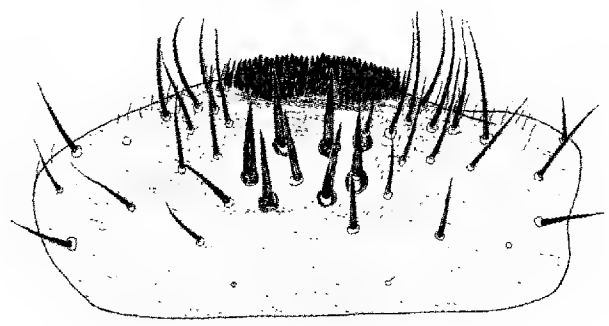
68 *Spelobia* ♂



69 *Afrolimosina* ♂



70 *Aptilotus* ♂

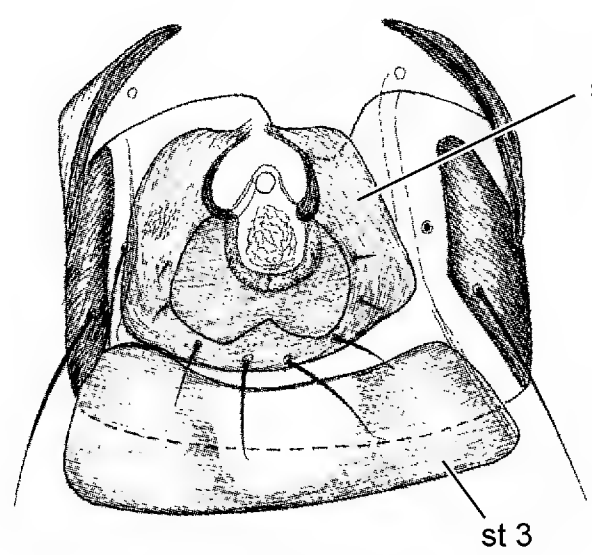


71 *Afropterogramma* ♂

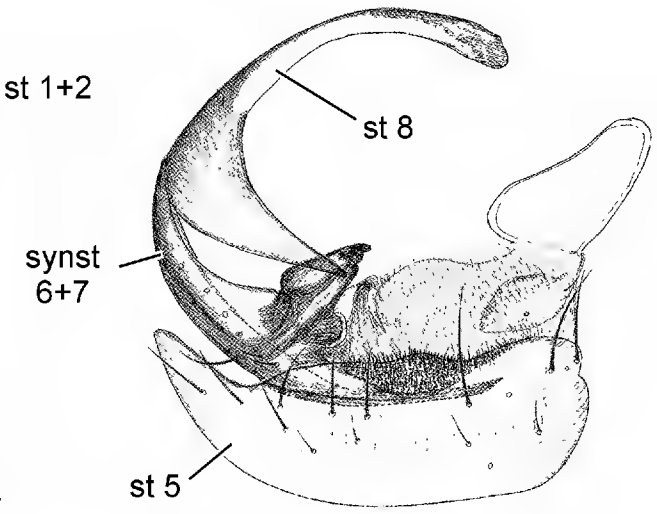
Figs 99.63–71. Male sternites 5 of Sphaeroceridae (ventral views): (63) *Piliterga thaii* L. Papp (non-Afrotropical); (64) *Mislocatus ealensis* (Vanschuytbroeck); (65) *Chaetopodella* (*Chaetopodella*) *denigrata* (Duda); (66) *Permixtolimosina sexsetosa* L. Papp; (67) *Acuminiseta ceropteroides* L. Papp; (68) *Spelobia talparum* (Richards) (non-Afrotropical); (69) *Afrolimosina albitarsis* L. Papp; (70) *Aptilotus beckeri* (Duda) (non-Afrotropical); (71) *Afropterogramma minor* L. Papp. Figs 63, 67, 71 (Papp 2008*b*, figs 36, 234, 78, respectively), Figs 64, 66, 69 (Papp 2014*a*, figs 54, 75, 2, respectively © Magnolia Press), Fig. 65 (Papp 2008*c*, fig. 8), Figs 68, 70 (Roháček 1983, figs 485, 411, respectively).

inventory of Afrotropical taxa. Consequently, the bibliographical knowledge and the nomenclatorial stability of the Sphaeroceridae are now in a satisfactory state.

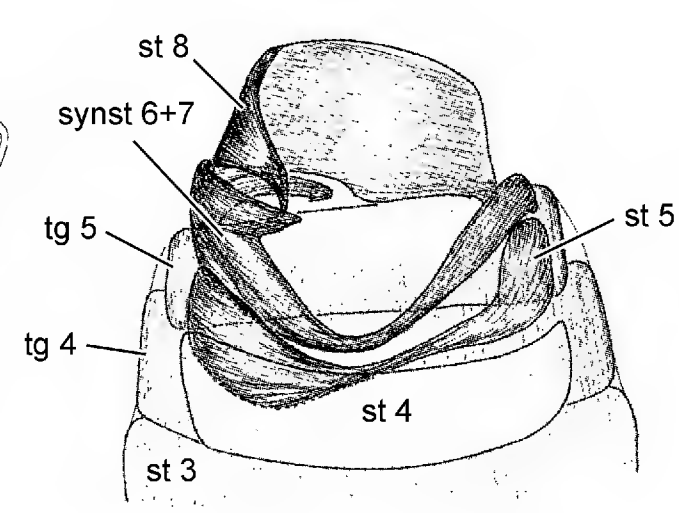
The only reliable fossil sphaerocerids were described from Dominican amber of Middle Miocene age (16–18 Mya), representing six species, all belonging to the subfamily Limosininae. Two of these were described, named and affiliated to the recent genera *Spelobia* Spuler and *Xenolimosina* Roháček. The remaining four species were left unnamed and only tentatively placed (Marshall *et al*. 1999). As Sphaeroceridae are not known from Eocene Baltic amber (Tschirnhaus & Hoffeins 2009), or from any other older amber deposits, the formerly supposed Cretaceous age (Roháček 1998) of the family is probably exaggerated. This statement can also be supported by the fact that no representative of any family of Acalyptratae (being otherwise very diverse in the Baltic amber) has hitherto been found in Cretaceous amber throughout the world.



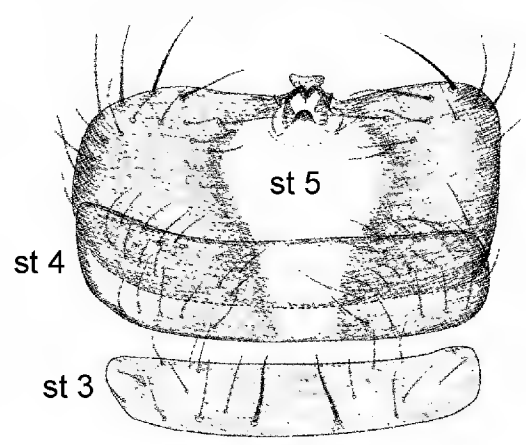
72 *Paraminilimosina* ♂



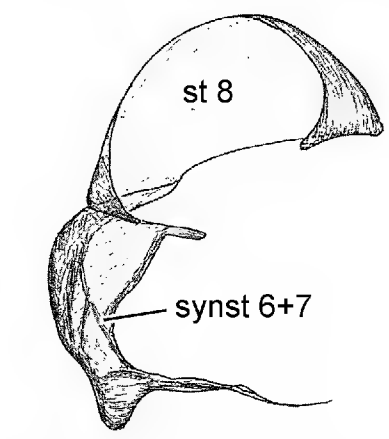
73 *Parapoecilosomella* ♂



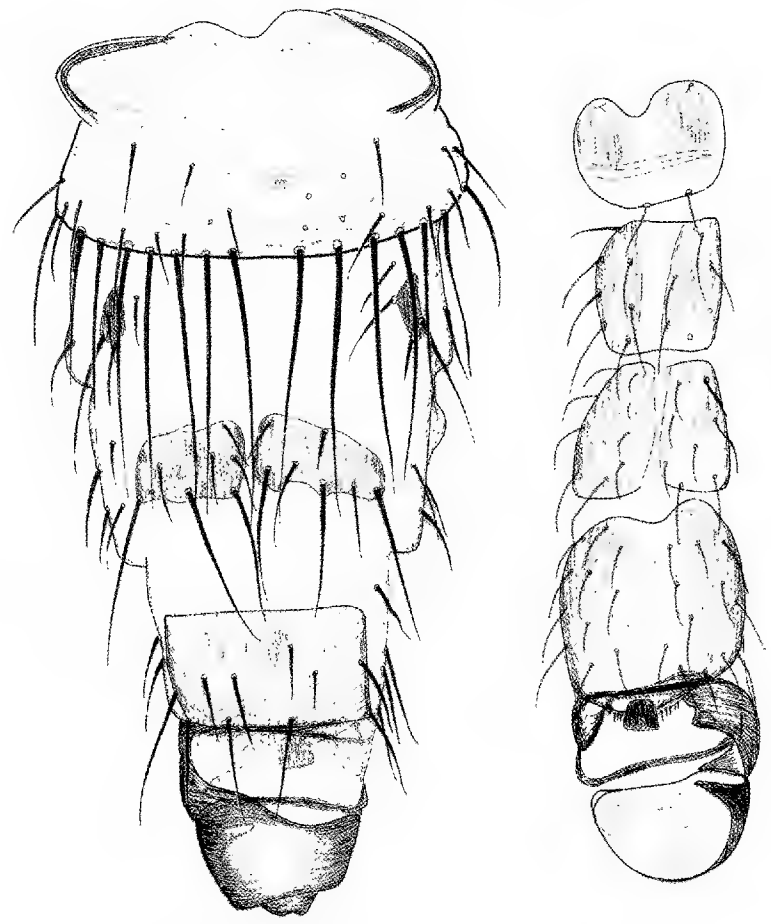
74 *Gonitella* ♂



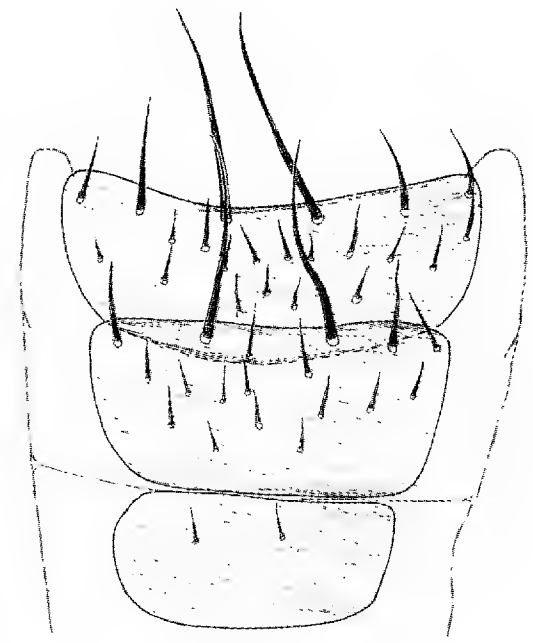
75 *Setositibiella* ♂



76 *Oligochaetosella* ♂



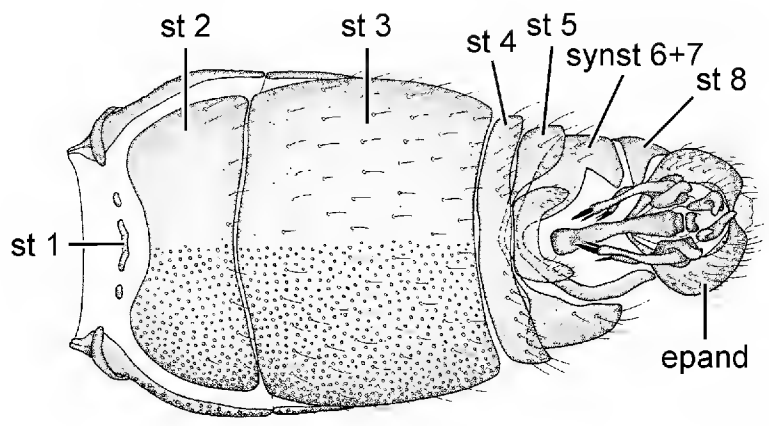
77 *Pseudaspinilimosina* ♂



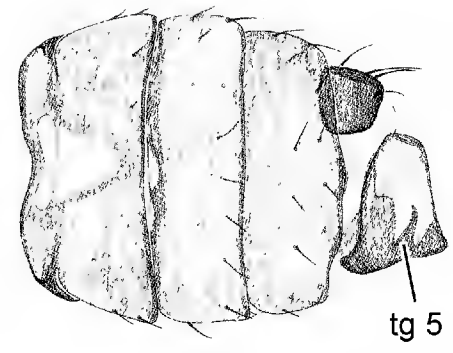
78 *Acuminiseta* ♂

Figs 99.72–78. Male abdominal segments, tergites and sternites of Sphaeroceridae (ventral views, unless otherwise stated): (72) sternites 2 and 3 of *Paraminilimosina miraculisterna* L. Papp; (73) sternite 5 and synsternite 6–8 of *Parapoecilosomella lusingana* (Vanschuytbroeck); (74) abdominal segments 4 and 5, with synsternite 6–8 of *Gonitella flavipes* L. Papp; (75) sternites 3 to 5 of *Setositibiella terrestris* L. Papp; (76) synsternite of *Oligochaetosella inconspicua* L. Papp; (77) abdominal tergites and sternites of *Pseudaspinilimosina tanzan* L. Papp, dorsal view (left), ventral view (right); (78) sternites 2 to 4 of *Acuminiseta ceropteroides* L. Papp. Figs 72–75, 77, 78 (Papp 2008*b*, figs 17, 106, 239, 287, 38, 39, 235, respectively), Fig. 76 (Papp 2014*a*, fig. 64 © Magnolia Press).

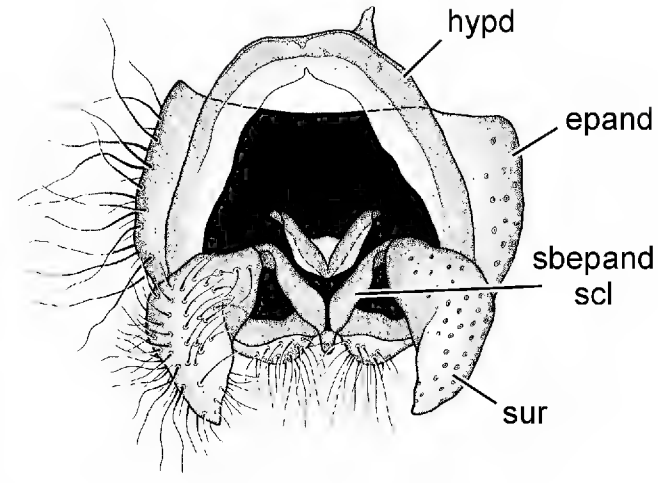
Abbreviations: st – sternite; synst – synsternite; tg – tergite.



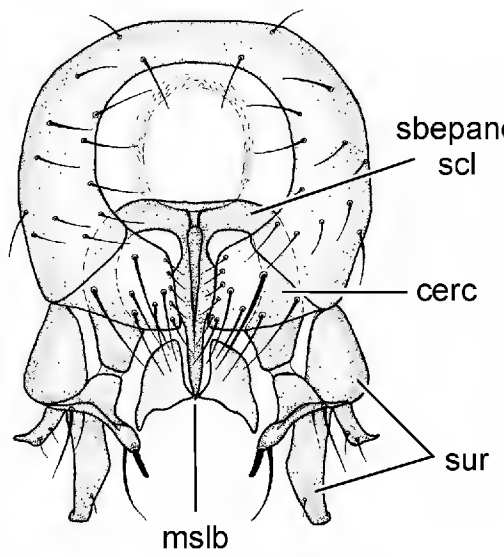
79 *Puncticorpus* ♂



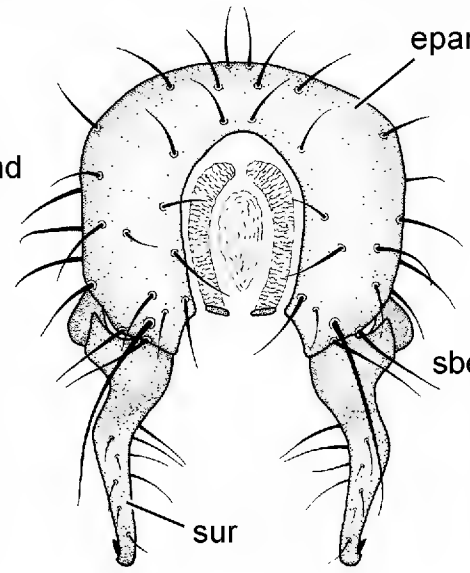
80 *Afropterogramma* ♂



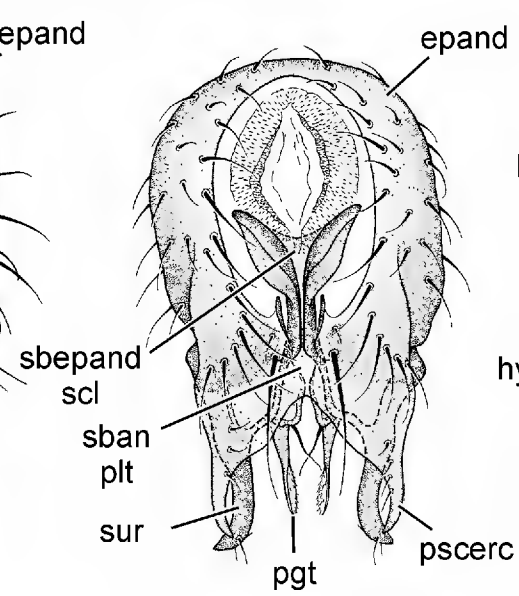
81 *Borborillus* ♂



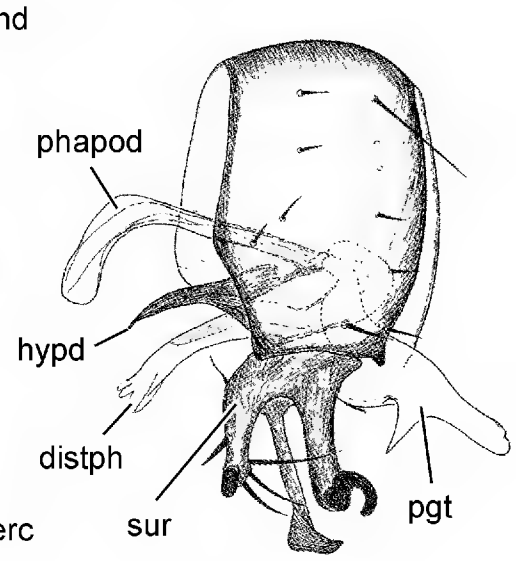
82 *Phthitia* (*Kimosina*) ♂



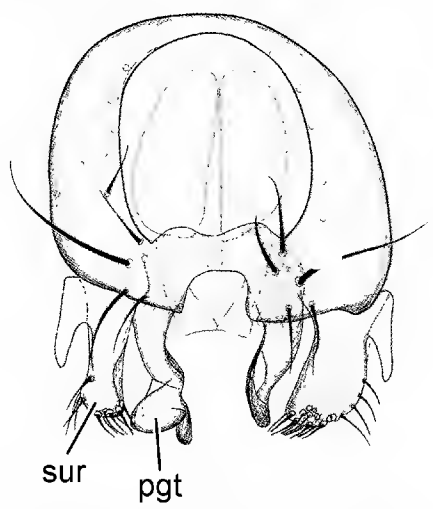
83 *Telomerina* ♂



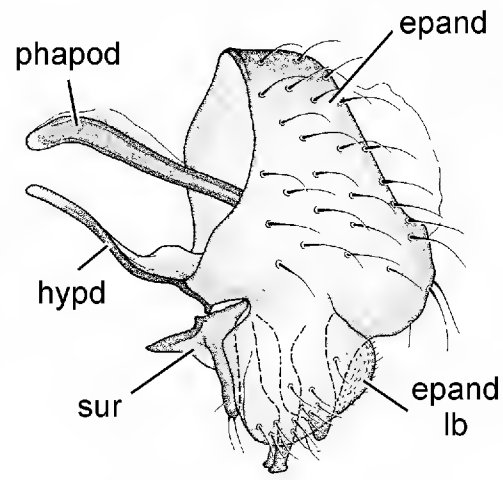
84 *Rachispoda* ♂



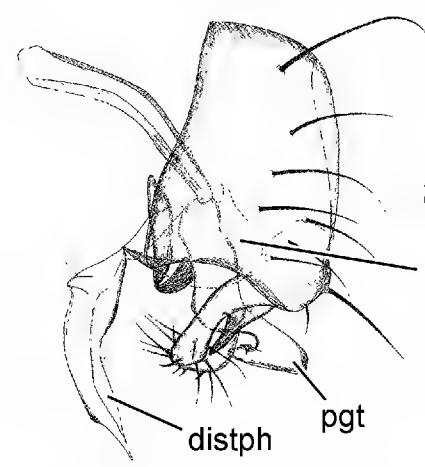
85 *Gonitella* ♂



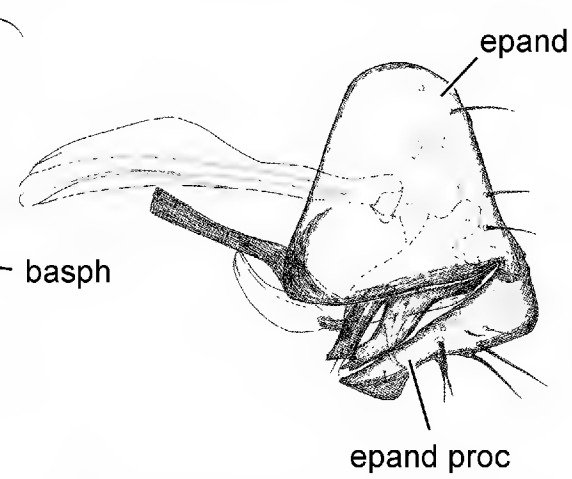
86 *Paracuminiseta* ♂



87 *Pseudocollinella* (*Pseudocollinella*) ♂



88 *Paracuminiseta* ♂



89 *Phthitia* (*Rufolimosina*) ♂

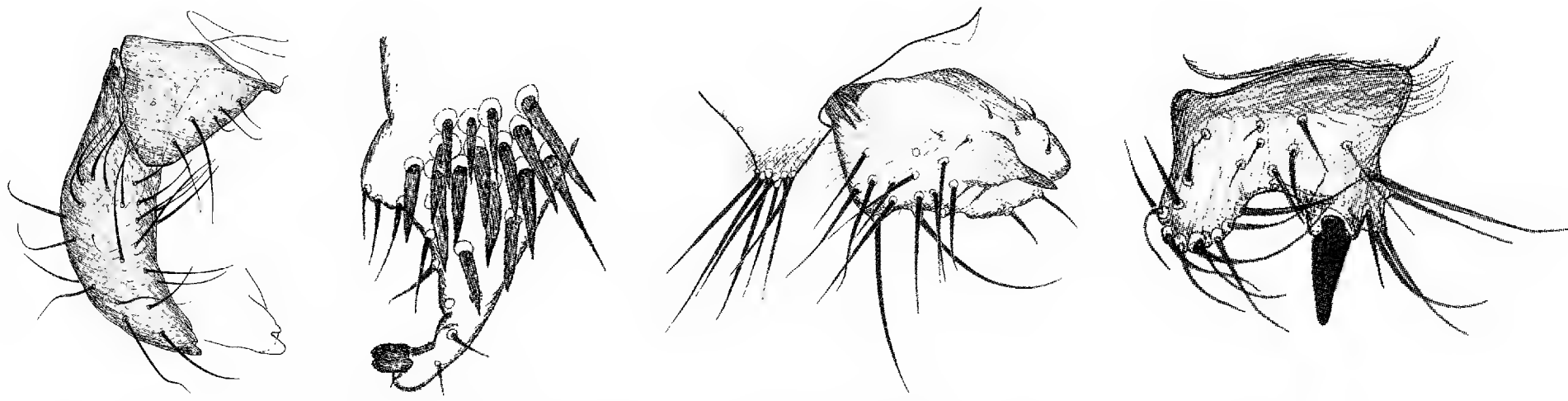
Figs 99.79–89. Male abdomens and terminalia of Sphaeroceridae: (79) abdomen of *Puncticorpus cribratum* (Villeneuve), ventral view (non-Afrotropical); (80) same (without terminalia) of *Afropterogramma minor* L. Papp, dorsal view; (81) terminalia (phallic complex removed), of *Borborillus vitripennis* (Meigen), ventral view (non-Afrotropical); (82) external terminalia of *Phthitia* (*Kimosina*) *plumosula* (Rondani), caudal view; (83) same, *Telomerina ursina* Roháček (non-Afrotropical); (84) same, *Rachispoda limosa* (Fallén) (non-Afrotropical); (85) terminalia of *Gonitella flavipes* L. Papp, lateral view; (86) external terminalia of *Paracuminiseta tetraspinosa* L. Papp, caudal view; (87) terminalia of *Pseudocollinella* (*Pseudocollinella*) *abhorrens* (Roháček), lateral view (non-Afrotropical); (88) same, *Pa. tetraspinosa*; (89) same, *Phthitia* (*Rufolimosina*) *oswaldi* L. Papp (non-Afrotropical). Figs 79, 81, 87 (Roháček 1998, figs 32, 35, 103), Figs 80, 85, 86, 88, 89 (Papp 2008*b*, figs 74, 242, 203, 205, 170, respectively), Figs 82, 83 (Roháček 1985, figs 879, 938), Fig. 84 (Roháček 1991, fig. 251).

Abbreviations: basph – basiphallus; cerc – cercus; distph – distiphallus; epand – epandrium; epand lb – epandrial lobe; epand proc – epandrial process; hypd – hypandrium; mslb – mesolobus; pgt – postgonite; phapod – phallapodeme; pscerc – pseudocercus; sban plt – subanal plate; sbepand scl – subepandrial sclerite; st – sternite; sur – surstylus; synst – synsternite ; tg – tergite.

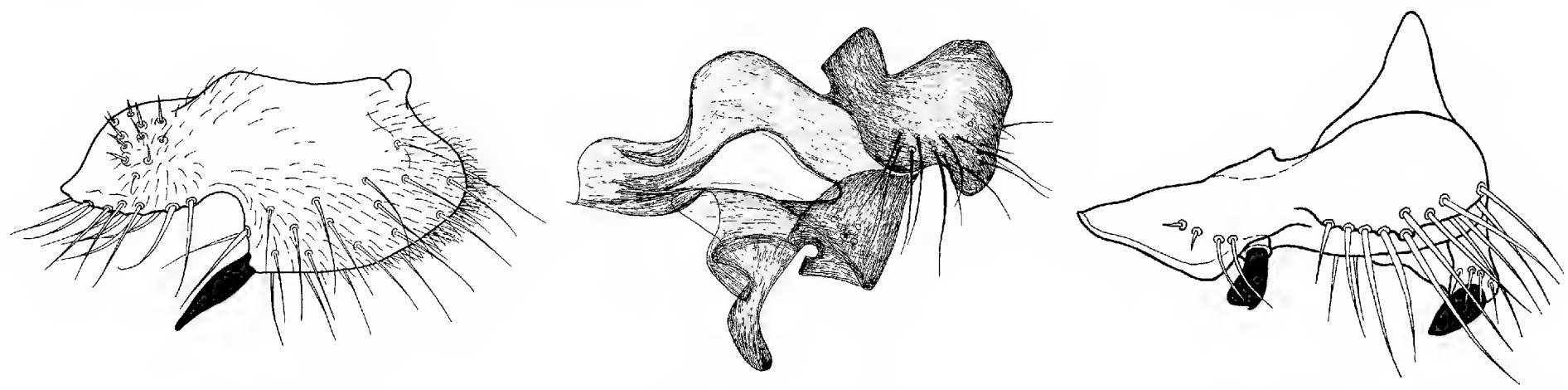
Identification

Roháček *et al*. (2001) listed 36 species of Limosininae as generically unplaced (*incertae sedis*), of which 15 are known from the Afrotropical Region. These species cannot be identified to genus and are not considered in this chapter and are not included in the below generic identification key.

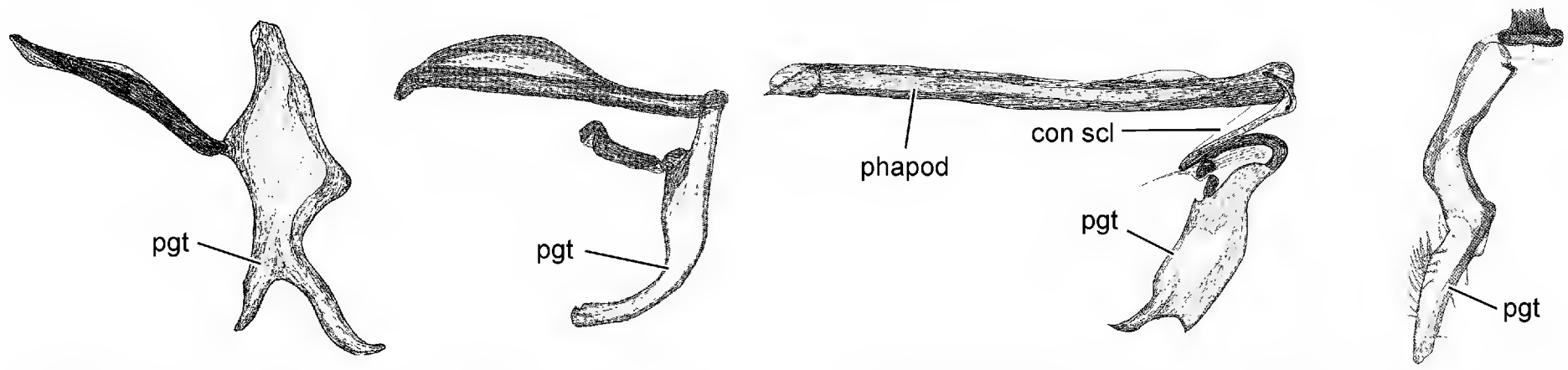
The identification key provided below was constructed by the senior author and is intended for the identification of both sexes



90 *Dudaia* ♂ 91 *Parapoecilosomella* ♂ 92 *Minilimosina* (*Sagittaliseta*) ♂ 93 *Bifronsina* ♂



94 *Spelobia* ♂ 95 *Paralimosina* ♂ 96 *Aptilotus* ♂



97 *Subacuminiseta* ♂ 98 *Paramera* ♂ 99 *Biphallapodema* ♂ 100 *Parapoecilosomella* ♂

Figs 99.90–100. Male terminalia of Sphaeroceridae: (90) left surstylus and cercus of *Dudaia flavocincta* (Duda), caudal view; (91) apical part of surstylus of *Parapoecilosomella lusingana* (Vanschuytbroeck), sublateral (widest extension) view; (92) surstylus of *Minilimosina* (*Sagittaliseta*) *siamensis* L. Papp, lateral view (non-Afrotropical); (93) same, *Bifronsina latitarsis* L. Papp, sublateral (widest extension) view; (94) same, *Spelobia palmata* (Richards), lateral view (non-Afrotropical); (95) same, *Paralimosina australis* L. Papp, sublateral (widest extension) view; (96) same, *Aptilotus beckeri* (Duda), lateral view (non-Afrotropical); (97) postgonite with hypandrial arm of *Subacuminiseta minor* L. Papp, lateral view; (98) postgonite and phallapodeme of *Paramera robusta* L. Papp, lateral view (non-Afrotropical); (99) same (with connecting sclerite) of *Biphallapodema polydentata* L. Papp; (100) left postgonite of *Parapoecilosomella lusingana*, caudal view. Fig. 90 (Papp & Norrbom 2015, fig. 12 © Magnolia Press), Figs 91–93, 98, 100 (Papp 2008*b*, figs 108, 161, 186, 69, 105, respectively), Figs 94, 96 (Roháček 1983, figs 476, 410, respectively), Fig. 95 (Papp 2013, fig. 29), Figs 97, 99 (Papp 2014*a*, figs 115, 33, respectively © Magnolia Press).

Abbreviations: con scl – connecting sclerite; pgt – postgonite; phapod – phallapodeme.

of Afrotropical Sphaeroceridae. There are several monotypic genera, however, that are based solely on males and in such cases the identification of congeneric females cannot be entirely certain.

If dealing with apterous or strongly reduced-winged species, go directly to couplet 13 (Limosininae); the only other short-winged species is *Safaria brachyptera* Richards, 1966, in which the thorax is clothed in numerous blunt setae on tubercles, which belongs to the subfamily Sphaerocerinae (couplet 3). Moreover, the wing of this species bears complete venation (see Richards 1966) in contrast to the reduced wings of Limosininae.

Several species of *Paralimosina* L. Papp may run to couplet 71. Hayashi (2008*a*, 2008*b*, 2012) described nine patterned winged species from Thailand, Malaysia and Vietnam and there are representatives of seven additional Oriental species known from collections (L. Papp, unpubl.). Although *Paralimosina* species with maculate wings are hitherto unknown from the Afrotropical Region, their occurrence in the region cannot be excluded. These *Paralimosina* species can be distinguished from other Afrotropical genera with patterned wings by the following combination of characters: preabdominal tergites and sclerites of segment 6 not reduced in size; male hypandrium with a ventral process; surstylus consisting of a larger cranial lobe, bare or with a few small setae and a smaller caudal lobe, with several long setae; postgonite not broad based, long curved with the apex seldom sharp; and surface of female spermathecae wrinkled.

The apterous genus *Ocellusia* Séguy may key to couplet 80. The mid tibia has a proximal anterodorsal seta and a pair of distal setae and the scutellum is long, with 2 pairs of long scutellar setae.

Sphaeroceridae are best micro-pinned in the field for later double-mounting (see Chapter 2).

Key to genera of Afrotropical Sphaeroceridae

1. Costal wing vein (*C*) extending to vein M_1; vein M_1 complete; with basal medial crossvein (*bm–m*) and anterior cubital cell (*cua*) (e.g., Figs 42, 51); female with 2 spermathecae (e.g., Fig. 137) 2

– Costal wing vein (*C*) extending to, or slightly beyond, vein R_{4+5}; vein M_1 mostly shortened, not reaching wing margin as true vein (e.g., Figs 44, 48); without basal medial crossvein (*bm–m*) and anterior cubital cell (*cua*); female usually with 3 spermathecae (e.g., Figs 134–136, 138) (LIMOSININAE). 13

2. Hind tibia without dorsal preapical seta; wing vein M_4 reaching wing margin (e.g., Fig. 51); thorax with scutal setae and setulae (e.g., Figs 8, 10, 12) mostly in form of short spines or warts (except in *Trichosphaerocera* L. Papp, Fig. 34); scutellum with small teeth on posterior margin (e.g., Figs 10, 13), or at least basal scutellar seta reduced (SPHAEROCERINAE). 3

– Hind tibia with long dorsal preapical seta (e.g., Figs 55, 56); wing vein M_4 not reaching wing margin (e.g., Fig. 42); thorax with scutal setae and setulae normal; scutellum with at least 2 pairs of scutellar setae (COPROMYZINAE) 8

3. Body clothed in long, thin setulae (Fig. 11), only margin of scutellum with 3 pairs of minute tubercles (Fig. 34); thorax with 2 discernible notopleural setae (Fig. 34); wing vein R_1 with row of setulae on dorsal surface (Fig. 51); legs setulose (Fig. 11); abdominal sclerites large and well-sclerotised, with tergites and sternites meeting laterally. . . . . *Trichosphaerocera* L. Papp

– Body clothed in short, thick setae, or blunt setae inserted on small tubercles (e.g., Fig. 13); thorax without notopleural setae; wing vein R_1 without setulae on dorsal surface; legs with short setae; abdominal sclerites various, but usually with distinct membranous parts between tergites and sternites 4

4. Scutellum with 1 pair of marginal (lateral) tubercles; body clothed in short setae (e.g., Fig. 8). 5

– Scutellum with at least 6 marginal tubercles; body with numerous small, blunt setae on tubercles (e.g., Figs 10, 12) 6

5. Scutum strongly convex, more or less narrowed anteriorly, with distinct collar-like pronotum; mesonotum posterolaterally and sometimes also in prealar area bulging; scutellum subtriangular; hind tibia without ventral apical spur. . . . . *Afromyia* Kim

– Scutum more or less flattened, without collar-like pronotum (Fig. 8); mesonotum not bulging as described above; scutellum subrectangular (Fig. 8); hind tibia with large, curved ventral apical spur (Fig. 8). . . . . *Sphaerocera* Latreille

6. Thorax with 2 rows of acrostichal setae; head above eye with 2 large processes (viewed laterally) (Figs 12, 13); scutellum with 6 marginal tubercles; postabdomen strongly modified in both sexes (Figs 12, 13) . . . . . *Safaria* Richards

– Thorax with 4 rows of acrostichal setae; head above eye without 2 large protuberances (viewed laterally) (e.g., Figs 10, 28); scutellum with 6 or (usually) more marginal tubercles; postabdomen not strongly modified in both sexes. 7

7. Scutellum with 6–10 marginal tubercles, with bases of lateral pair never fused; wing vein M_1 straight; male terminalia with surstylus mostly straight, only slightly medially directed (in caudal view). . . *Ischiolepta* Lioy

– Scutellum with 11 or more marginal tubercles, bases of lateral pairs may be fused (Fig. 10); wing vein M_1 strongly upcurved (Fig. 10); male terminalia with surstylus markedly medially directed (in caudal view) . . . . . *Lotobia* Lioy

8. Hind tibia with distinct anteroventral seta distal to mid length (Fig. 56). . . . . *Norrbomia* L. Papp

– Hind tibia without distinct anteroventral seta (e.g., Fig. 9) 9

9. Scutellar margin with several thin setae between apical and lateral scutellar setae (Fig. 36); hind tibia without anterodorsal and anteroventral rows of short, erect setae (Fig. 9) . . . . . *Copromyza* Fallén

– Scutellar margin without thin setae between apical and lateral scutellar setae; hind tibia with anterodorsal and anteroventral row of short, erect setae 10

10. Hind tibia without curved ventral apical spur (Fig. 14); thorax mostly without acrostichal setae; wing with some non-microtrichose areas . . . . . *Achaetothorax* Hedicke

– Hind tibia with curved ventral apical spur; thorax with acrostichal setae invariably well-developed . . . 11

11. Antennal postpedicel conical or apically narrowed; arista apical or subapical (Fig. 2); hind tibia not strongly swollen; wing without non-microtrichose areas . . . . . *Dudaia* Hedicke

– Antennal postpedicel more rounded; arista dorsal (e.g., Fig. 1); hind tibia often strongly swollen, with long curved ventral apical spur; wing mostly with non-microtrichose areas. 12

12. Scutellum with basal pair of scutellar setae almost as long as apical scutellar setae; wing vein M_4 with terminal section (distal to cell *dm*) always present; legs bicolourous . . . . . *Gymnometopina* Hedicke

– Scutellum with basal scutellar setae much shorter than apical scutellar setae; wing vein M_4 with terminal section (distal to cell *dm*) frequently lacking; legs unicolourous. . . . . *Metaborborus* Vanschuytbroeck

13. Wings and halteres present, mostly of normal size; if wings shortened, then venation still clearly visible 14

– Wings and/or halteres absent or greatly reduced; if wings shortened, venation invariably reduced (not visible) 76

14. Tarsi with pulvilli and claws considerably enlarged (Figs 16, 22), or if claws reduced, substituted by long apical lateral lobes of tarsomere 5; hind tibia with short, but robust, ventroapical spur (e.g., Fig. 54); head with frons long, usually with numerous interfrontal setulae (e.g., Fig. 31); abdominal tergites and sternites in many species rudimentary, but in such cases marginal setae of tergites not extremely long; male terminalia with pair of large ventral (ventromedial) epandrial processes, surstylus inserted between epandrium and processes (Papp 2014*b*, fig. 29) 15

– Tarsi with pulvilli and claws weakly developed (except fore claws in *Chelilimosina* L. Papp and *Pseudacuminiseta* L. Papp); hind tibia with ventroapical spur mostly reduced; head with frons shorter, with a few interfrontal setae (e.g., Figs 27, 29, 30); abdominal tergites and sternites well-sclerotised, if tergites reduced, then marginal setae extremely long; male terminalia not as described above 16

15. Thorax with 0 + 1–2, or 1 + 2 dorsocentral setae and usually numerous (6–8) rows of acrostichal setae; head with ocellar setae well-developed; with numerous, but weak interfrontal setae (Fig. 31); ocellar triangle either small, or not shiny; position of ocelli normal, without postocellar setae; inner vertical seta inserted close to outer vertical seta (Fig. 31); lunule small, bare or only finely setulose (Fig. 31); abdominal tergites reduced, but sternites 1–4 never entirely de-sclerotised. . . . . *Ceroptera* Macquart

– Thorax with 1 + 1 robust dorsocentral setae and 3 (4) rows of irregularly arranged acrostichal setae; head without ocellar setae; with 4 comparatively large interfrontal setae; ocellar triangle large and shiny, extending anteriorly so that anterior ocellus situated near middle of frons; postocellar setae well-developed; inner vertical seta inserted well anterior to outer vertical seta; lunule large and setose; abdominal sternites 1–4 and tergite 3 not sclerotised, tergite 4 represented by 2 minute sclerites (Papp 1977, figs 5, 6). . . . . *Ceropterella* Richards

16. Scutellum with at least 1 pair of small setulae inserted between apical scutellar setae (e.g., Figs 38, 39); scutellar disc more or less setulose, with at most 2 pairs of long scutellar setae (e.g., Figs 38, 39); wing with first costal sector (basicosta to vein R_1) short-haired. 17

– Scutellum without setulae inserted between apical scutellar setae (e.g., Fig. 37); scutellar disc usually bare, but if setulose (e.g., Fig. 37), then with at least 3 pairs of long marginal scutellar setae; wing with first costal sector (basicosta to vein R_1) sparsely long-setose (e.g., Fig. 44) 18

17. Scutellar disc densely setulose (Fig. 38); wing vein *CuA+CuP* angulate. . . . . *Coproica* Rondani

– Scutellar disc not densely setulose, with 2 pairs of small setulae only (Fig. 39); wing vein *CuA+CuP* sinuate. . . . . *Philocoprella* Richards

18. Mid tibia with distinct ventral preapical seta (e.g., Fig. 59), or if without long seta ventrally, then mid tarsomere 1 invariably with distinct ventral seta 19

– Mid tibia without ventral preapical seta, but usually with ventroapical seta (e.g., Fig. 61), sometimes reduced in males and long ventral seta on mid tarsomere 1 only present in species with distinct ventroapical seta on mid tibia (e.g., Fig. 57) 22

19. Scutellum with 3–4 pairs of marginal setae (e.g., Fig. 37); scutellar disc setulose in some species; mid trochanter with long upcurved seta (e.g., Fig. 59); mid tibia with ventral preapical seta always present (e.g., Fig. 59) 20

– Scutellum with only 2 long pairs of marginal setae; scutellar disc invariably bare; mid trochanter with or without short seta; mid tibia with ventral preapical seta sometimes present in females 21

20. Thorax with foremost dorsocentral seta directed posteriorly; head with facial carina never protruding between antennae; scutellum invariably with 4 pairs of marginal setae; male terminalia with epandrium not fused below anal fissure and pair of processes (pseudocercus = posterior projection of epandrium or modified cercus) separate from epandrial complex (Fig. 125). . . . . .*Leptocera* Olivier

– Thorax with foremost dorsocentral seta inclinate (Fig. 35), if reclinate, then facial carina strongly bulging between antennae; scutellum with 3–7 pairs of marginal setae (Figs 35, 37); male terminalia with epandrium fused below anal fissure forming subanal plate and pair of processes coalesced with epandrial complex (Fig. 84). . . . . *Rachispoda* Lioy

21. Thorax with 1–3 dorsocentral setae, all postsutural; wing with first costal sector (basicosta to vein R_1) usually with short setae; male terminalia with surstylus simple, epandrium without lateral process overlapping surstylus; basiphallus with posteriorly projecting epiphallus (Fig. 121). . . . . .*Opacifrons* Duda

– Thorax with 3 or more dorsocentral setae, at least 1 presutural; wing with first costal sector (basicosta to vein R_1) usually with long setae; male terminalia with surstylus bipartite and complex, with posterior part more or less covered by ventrolateral process or lobe of epandrium (Fig. 87); basiphallus simple (Fig. 112). . . . . .*Pseudocollinella* Duda

22. Head with lateroclinate or inclinate inner fronto-orbital setae inserted between interfrontal setae and fronto-orbital setae (e.g., Fig. 27); small or very small species (body length: 0.7–1.3 mm). 23

– Head without inner fronto-orbital setae, at most with several minute additional lateroclinate setulae inserted close to fronto-orbital setae (e.g., Fig. 26); mostly larger species (body length: > 1.5 mm) 27

23. Head with distinct row of inclinate inner fronto-orbital setae (e.g., Fig. 27); wing with alula large, rounded apically (e.g., Fig. 43); vein R_{4+5} variable (curved or sinuate) 24

– Head with reduced number of lateroclinate inner fronto-orbital setae (with at least 1 longer and 1 or 2 smaller setae) between interfrontal setae and fronto-orbital setae; wing with alula small and narrow (e.g., Fig. 53); vein R_{4+5} strongly curved up to costal vein (*C*) (e.g., Fig. 53) 25

24. Wing vein R_{4+5} very strongly curved up to costal vein (*C*); vein *CuA+CuP* more or less distinctly angulate; without strong basal costagial seta, but costal vein (*C*) with erect setulae, perpendicular to alar plane; head with inner fronto-orbital setulae inserted farther from fronto-orbital setae; male sternite 5 with lateral spinelets or combs of setae . . . . . *Elachisoma* Rondani

– Wing vein R_{4+5} bisinuate (Fig. 43); vein *CuA+CuP* gently sinuate; with large, inclinate, posteriorly directed costagial seta (Fig. 43); costal vein (*C*) without erect setulae; head with inner fronto-orbital setulae inserted close to fronto-orbital setae; male sternite 5 with single medial comb of setae . . . . . .[*Gonioneura* Rondani]

25. Compound eye distinctly pilose; thorax with medial (internal) postpronotal seta relatively long, only slightly shorter than external seta . . . . . .*Trachyopella* (*Trachyopella* Duda)

– Compound eye apparently bare (e.g., Fig. 27); thorax with medial (internal) postpronotal seta much shorter than external seta. 26

26. Head (Fig. 27) and mid tibial setae robustly developed; wing broader (Fig. 53); vein R_{2+3} to costal vein (*C*) not at such acute angle (Fig. 53); abdominal tergites 4 and 5 (in female also tergite 6) with strong setae in posterior corners; male terminalia with surstylus short and wide, with single robust spine on posterior lobe; female paired spermathecae with sclerotised parts of ducts not closely connected . . . . . .*Nudopella* Roháček & Marshall

– Head and mid tibial setae weakly developed; wing narrower (Fig. 52); vein R_{2+3} connected to costal vein (*C*) at very acute angle (Fig. 52); abdominal tergites 4 and 5 with short setulae; male terminalia with surstylus long and narrow, with at least 2, but often more, robust spines; female paired spermathecae with sclerotised parts of ducts closely connected . . . . . *Trachyopella* (*Insulomyia* L. Papp)

27. Body heavily sclerotised or even distinctly granulose (abdomen in particular); male terminalia with postgonites either asymmetrical or very large (e.g., Figs 85, 113, 114) 28

– Body usually less sclerotised, not granulose, but if so (some *Aptilotus* Mik and *Paralimosina*), then male terminalia with postgonites symmetrical and of normal size (e.g., Figs 97–100, 118). 30

28. Body granulose, subshiny to (abdomen) shiny; thorax with prosternum broadly triangular posteriorly; abdominal sternite 3 long (Fig. 79), invariably as long as tergites 3 and 4 combined; male terminalia with postgonites asymmetrical (Fig. 113) (not recorded from Afrotropical Region). . . . . .[*Puncticorpus* Duda]

– Body not granulose, subshiny; thorax with prosternum narrow; abdominal sternite 3 not as long as tergites 3 and 4 combined; male terminalia with postgonites symmetrical but large (e.g., Figs 85, 114). 29

29. Wing rather narrow; second costal sector (veins R_1 to R_{2+3}) much longer than third sector (veins R_{2+3} to R_{4+5}); male mid tibia without long ventral hair-like setae; sternite 5 asymmetrical and heavily sclerotised (Fig. 74); male terminalia with postgonite extremely large and straight, with long medial anterior process (Fig. 85). . . . . .*Gonitella* L. Papp

– Wing broad and rounded, second costal sector (veins R_1 to R_{2+3}) only *ca* ½ length of third sector (veins R_{2+3} to R_{4+5}); male mid tibia with very long ventral hair-like setae; sternite 5 symmetrical (Fig. 75); male terminalia with postgonite curved, with small medial anterior process (Fig. 114) . . . .*Setositibiella* L. Papp

30. Wing membrane unicolourous, at most infuscate over crossveins, or if entire membrane with pale, cloudy colouration (*Acuminiseta* Duda, Fig. 18), then head with 1 fronto-orbital seta. 31

– Wing membrane distinctly patterned (e.g., Figs 19, 40, 47) and head with 2 or more fronto-orbital setae 71

31. Abdominal tergites reduced and de-sclerotised (sub-membranous) and with extremely long marginal setae (e.g., Fig. 77). 32

– Abdominal tergites not reduced, but if so, then these with markedly shorter marginal setae 37

32. Hind tibia with very thick spurs apically; head with postocellar setae very strong 33

– Hind tibia without thick apical spurs, but sometimes with ventral preapical spur (then postocellar setae small); head with postocellar setae variable in length 34

33. Costal wing vein (C) extended beyond apex of vein R_{4+5}; hind tarsus with all tarsomeres broadened (thickened); head with inner occipital seta reduced; thorax with 2 dorsocentral setae, the anterior strong; hind tibia with anterior or anteroventral spur, plus 1 dorsal/anterodorsal preapical spine; mid tibia with distinct ventroapical spur . . . . . .*Aspinilimosina* L. Papp

– Costal wing vein (C) just reaching apex of vein R_{4+5}; hind tarsus with only tarsomeres 1 and 2 thickened; head with inner occipital seta distinct; thorax with 3 dorsocentral setae, although anterior 2 short; both mid and hind tibiae with short ventroapical spur . . . . . *Pseudaspinilimosina* L. Papp

34. Fore femur proximally with 2 pairs of long ventral setae; head with 6 interfrontal setae and very strong postocellar setae; mid tarsomere 1 with rows of strong anteroventral and posteroventral setae. . . . . .*Chaetosifemur* L. Papp

– Fore femur without long paired setae proximally; other characters not in above combination. 35

35. Mid tibia with posterodorsal seta at basal ½; costal wing vein (C) ending at apex of vein R_{4+5}; abdominal sternite 1 + 2 normal; male sternite 5 with posteromedial area bearing irregular rows of short stiff setae (Fig. 63). . . . . .*Piliterga* L. Papp

– Mid tibia without posterodorsal seta in basal ½; costal wing vein (C) reaching beyond apex of vein R_{4+5}; abdominal sternite 1 + 2 normal or modified (Fig. 72); male sternite 5 with armature not as above 36

36. Head without distinct anterior genal seta; postocellar setae indistinct; wing with alula of medium length, with apex rounded; subcostal vein (*Sc*) conspicuous, clearly discernible up to ⅘ length of vein R_1; mid tibia dorsally with only 2 anterodorsal setae above long subapical anterodorsal seta; abdominal sternite 1 + 2 unmodified; male sternite 5 with pair of posterior projections, each bearing transverse setal comb (Fig. 64). . . . . .*Mislocatus* L. Papp

– Head with anterior genal seta short, but distinct; postocellar setae long; wing with alula small and narrow; subcostal vein (*Sc*) inconspicuous, not clearly discernible; mid tibia with additional long setae dorsally, including distal posterodorsal seta; abdominal sternite 1 + 2 with peculiar structure (Fig. 72); male sternite 5 without paired projections, with combs of short setae . . . . . .*Paraminilimosina* L. Papp

37. Scutum with 4–6 dorsocentral setae, including 1 or 2 anterior (presutural) inclinate setae (Fig. 15); wing with first costal sector (basicosta to vein R_1), with long, sparse setae (Fig. 15); male terminalia with

surstyli short (low), usually bilobed, with spine(s) on posterior lobe; male cerci not, or only slightly, projecting ventrally . . . . . *Thoracochaeta* Duda

– Scutum with 1–6 dorsocentral setae, if presutural dorsocentral setae present, then these directed posteriorly; wing with first costal sector (basicosta to vein R_1) with setae variable, but usually small and dense; male terminalia with surstyli and cerci not as described above 38

38. Antennal postpedicel strongly conical with acute apex (e.g., Fig. 33), or even with small rod-like projection (e.g., Fig. 32); arista with long pubescence (plumose) (e.g., Figs 32, 33); male fore tarsal claws normal; male terminalia with surstylus never with long sinuate setae 39

– Antennal postpedicel not conical, but if slightly so, then never with rod-like projection; other characters not in above combination 41

39. Head with 4 (rarely 3) small or medium-long interfrontal setae; postocellar setae small, but distinct; thorax with 1 dorsocentral seta, plus an oblique row of small setae more anteriorly; costal wing vein (C) thickened, with long setae on first costal sector (basicosta to vein R_1) and rather long dorsal and ventral setulae along length; male mid tibia with row of strong, short ventral setae; female mid tibia with small mid ventral (anteroventral) seta; abdominal tergites 1 and 2 modified in some species; female cercus often with 1 or more thick spines; spermathecae globular, single spermatheca not (or only slightly) larger than paired spermathecae . . . . . *Anommonia* Schmitz

– Head with 2 strong interfrontal setae (or 1 strong anterior + 1 small posterior); postocellar setae absent; thorax with 1 or 2 strong dorsocentral setae; costal wing vein (C) thickened or not, but invariably with short setae on first costal sector (basicosta to vein R_1); mid tibia in both sexes without ventral setae; abdominal tergites 1 and 2 simple; female cercus with thin setae and setulae; spermathecae variable 40

40. Scutum with 2 strong dorsocentral setae; costal wing vein (C) not markedly thickened; male mid tibia with row of long, hair-like anteroventral setae; male terminalia with surstylus bilobed, with lateral lobe small, slender, pointed and bare, medial lobe larger and setose (Fig. 86); postgonite curved caudally, but apically recurved, without processes (Fig. 88); basiphallus and distiphallus flat (Figs 88, 123); female postabdomen with small triangular epiproct; cercus with 3 thin straight setae and fine setulae; spermathecae unequal (1 large plum-shaped spermatheca and 2 smaller longish paired spermathecae); spermathecal duct not sclerotised . . . . . *Paracuminiseta* L. Papp

– Scutum with 1 strong dorsocentral seta; costal wing vein (C) markedly thickened; male mid tibia without row of anteroventral setae; male terminalia with surstylus simple, with tapered apex, bearing spine-like seta; postgonite large with 2 long apical processes (Fig. 97); basiphallus and distiphallus robust, each with large ventral process (Fig. 119); female postabdomen with very weak, transverse epiproct and transverse cerci with very short curved setae; spermathecae subequal; spermathecal duct short and sclerotised in paired spermathecae . . . . . *Subacuminiseta* L. Papp

41. Large-headed, robust flies, with a broad scutellum; head with 4–5 pairs of short interfrontal setae; with strong upcurved genal seta; postocellar setae weak (but inner or both occipital setae may be strong); thorax with 1 dorsocentral seta; wing (e.g., Fig. 50), with relatively long setae on first costal sector (basicosta to vein R_1); vein R_{4+5} strongly upcurved, with apex ending far from wing tip, where costal vein (C) ends; alula narrow 42

– Without above combination of characters 45

42. Mid tibia without mid ventral seta; mid tarsomere 1 with longer posteroventral seta in basal $\frac{1}{3}$–$\frac{2}{5}$; mid tibia with paired setae present on dorsobasal $\frac{1}{2}$; male mid tibia with ventroapical seta short, but with row of short, thick ventral setae in apical $\frac{3}{5}$ (female without such setae, but ventroapical seta longer); hind tibia with long dorsal preapical seta; head with genal seta situated farther from mouth margin and more or less strong; gena broad, but without subocular setae; wing cell *dm* rounded; male terminalia with extremely large postgonites (Fig. 98) . . . . . *Paramera* L. Papp

– Mid tibia with mid ventral seta; mid tarsomere 1 without longer seta posteroventrally; male mid tibia with strong ventroapical seta, but without ventral row of thick setae (e.g., Fig. 61); hind tibia with dorsal preapical seta indistinct; head with genal seta long; wing cell *dm* rounded or angular; male terminalia with postgonites short 43

43. Mid tibia with 1 or 2 posterodorsal setae in basal $\frac{1}{2}$, *i.e.*, paired setae present (Fig. 60); wing cell *dm* rounded or angulate with M_1 vein appendage barely discernible; antennal scape with medial seta large, as long as pedicel; male terminalia with surstylus low (short), with strong thick spine on posterior lobe (Fig. 109); postgonite base very broad, apical $\frac{1}{2}$ narrowed and anteriorly curved (not recorded from Afrotropical Region) . . . . . [*Eximilimosina* L. Papp]

– Mid tibia without posterodorsal seta on basal $\frac{1}{2}$, *i.e.*, anterodorsal setae unpaired; wing cell *dm* angulate, with short M_1 vein appendage (Fig. 50); antennal scape with medial seta minute, at least much

shorter than pedicel; male terminalia with surstylus as long as broad, with larger external and smaller internal lobes, the latter with thickened seta; postgonite not dilated basally . . . . . *Spinilimosina* Roháček *sensu lato* 44

44. Head with gena not broad; genal setulae behind genal seta long, inserted closer to mouth margin; subocular setae absent or short; antennal arista usually with short pubescence; wing with costagial seta short; male terminalia with dorsal appendage of phallus not longer than phallus length . . . . . *Spinilimosina sensu stricto* [in part]

– Head with gena very broad; genal setulae behind genal seta short, inserted farther from mouth margin; subocular setae long; antennal arista with very long pubescence, plumose (length of cilia > 0.02 mm); wing with at least 1 very long dorsal costagial seta (as in *Gonioneura*); male terminalia with dorsal appendage of phallus longer than phallus length . . . . . *Spinilimosina* (undescribed subgenus)

45. Scutellum velvety black micro-tomentose; mid tarsomere 1 with distinct anteroventral seta (Fig. 57); male abdominal sternite 5 with pair of digitiform projections (Fig. 65) . . . . . *Chaetopodella* Duda

– Scutellum not velvety black micro-tomentose; mid tarsomere 1 usually without long anteroventral seta, but if present, then male abdominal sternite 5 not as described above 46

46. Scutum with 3–6 dorsocentral setae, those presutural usually small; wing vein R_{4+5} sinuate or virtually straight; compound eye not reduced 47

– Scutum usually with only 1 or 2 dorsocentral setae, if 3 present, then wing vein R_{4+5} slightly recurved (e.g., Fig. 41) or compound eye strongly reduced 48

47. Thorax with 3 dorsocentral setae (1 presutural and 2 postsutural setae); katepisternum with 2 setae, the anterior long; mid tibia with distinct mid ventral seta; head with facial carina bulging between antennae; antennal foveae deep, due to protruding lower facial margin; male terminalia with cerci ventrally projecting as narrow, posteriorly slightly curved bare processes; subepandrial sclerite small and simple; surstylus simple (Wheeler & Marshall 1991, figs 25, 26); spermathecae with 2 invaginations each . . . . . *Archicollinella* Duda

– Thorax with 3–6 dorsocentral setae (0–3 presutural and 3 postsutural setae); katepisternum with anterior seta much shorter and weaker than posterior seta; head with facial carina small; antennal foveae shallow; mid tibia with (at most) small mid ventral setula; male terminalia with cerci never forming bare narrow processes; subepandrial sclerite usually projecting ventrally, forming a medial mesolobus (Fig. 82); surstylus complex, bipartite (Fig. 82); spermathecae simple, without invaginations . . . . . *Phthitia* (*Kimosina* Roháček)

48. Scutellum with 3 pairs of marginal setae (basal setae short); mid tarsomere 1 with 1 stronger subbasal posteroventral seta; compound eye 2 × higher than gena; wing vein R_{4+5} strongly upcurved; male sternite 5 large (Fig. 66), with pair of broad closely approximated mediocaudal processes with pegs of setae; male terminalia with subepandrial sclerite extremely large; surstylus elongate and very slender; hypandrium small and basiphallus with anterior projection; female postabdomen with epiproct well-developed, with a pair of longer setae; cercal setae extremely long and spermathecae tyre-shaped, with conical part basally . . . . . *Permixtolimosina* L. Papp

– Scutellum usually with 2 pairs of marginal setae; mid tarsomere 1 without posteroventral seta; compound eye > 2 × height of gena, or if smaller, then all other characters differ 49

49. Male terminalia with epiphallus distinctly developed (e.g., Figs 115, 120); female postabdomen with epiproct short, mostly reduced, often fused with cerci; body heavily micro-tomentose, rather dull; thorax with mesonotum somewhat opalescent 50

– Male terminalia with epiphallus not developed, but pre-epiphallus sometimes present; female postabdomen with epiproct discrete, not fused with cerci; body (including mesonotum) usually more shiny, despite some micro-tomentum 51

50. Male fore tarsus with outer claws very large (Fig. 58); wing with costal vein (C) not developed beyond apex of vein R_{4+5}; hind tibia with ventral spur indistinct; male terminalia with distiphallus large, with long ventral apical appendices; basiphallus vertical, with epiphallus small (Fig. 120); female spermathecal ducts bulbous, very close to body of spermathecae (Fig. 138) . . . . . *Chelilimosina* L. Papp

– Male fore tarsus with outer claws normal; wing with costal vein (C) distinctly produced beyond apex of vein R_{4+5}; hind tibia with ventral spur distinct to very long; male terminalia with distiphallus without long ventral apical appendages; basiphallus with epiphallus long (Fig. 115); if spermathecal ducts bulbous, then dilated part distant from body of spermatheca . . . . . *Opalimosina* Roháček

51. Costal wing vein (C) distinctly developed beyond apex of vein R_{4+5} (e.g., Fig. 46) 52

– Costal wing vein (C) not, or very shortly, produced beyond apex of vein R_{4+5} (e.g., Figs 49, 50) 61

52. Wing vein R_{4+5} either virtually straight, or strongly curved up to costal vein (*C*) (rarely slightly bent or sinuate, but if so, then male terminalia with surstylus long and slender); female postabdomen short, as wide as preabdomen at segment 5, then abruptly tapered apically, not telescopic (*e.g.*, Fig. 129) 53

– Wing vein R_{4+5} sinuate or slightly bent up to costal vein (*C*); male terminalia with surstylus never long and slender; female postabdomen usually long and narrow, essentially narrower than preabdomen at segment 5, then gradually tapered apically and telescopically retractable (*e.g.*, Figs 128, 130) 56

53. Wing vein R_{4+5} virtually straight or very slightly sinuate, or if somewhat bent, then wing never reduced 54

– Wing vein R_{4+5} strongly curved up to costal vein (*C*) and ending farther from wing apex than virtual continuation of vein M_1 would do, or wing reduced and vein R_{4+5} straighter; rarely vein R_{4+5} less curved, but then scutellum with additional setulae 55

54. Wing membrane darkened, but not patterned (wing may be reduced in dimorphic species); head without postocellar setae; compound eye normal; male terminalia with subepandrial sclerite and epandrium ventrally closed; surstylus short but bilobed; postgonite bare . . . . . *Limosinella* Richards

– Wing membrane hyaline (wing never reduced); head with postocellar setae relatively strong; compound eye small and flat; male terminalia without subepandrial sclerite and epandrium ventrally open (Fig. 83); surstylus very long and slender (Fig. 83); postgonite finely pilose . . . . . *Telomerina* Roháček

55. Scutellum with additional short basal marginal seta; male terminalia with surstylus long and slender; female postabdomen with epiproct greatly reduced or wholly membranous; spectacles-shaped sclerite highly modified, *i.e.*, not present in typical form; spermathecae long, not tyre-shaped (not recorded from Afrotropical Region). . . . . [*Chespiritos* Marshall]

– Scutellum without additional basal marginal seta; male terminalia with surstylus roughly quadrate to triangular (Fig. 101); female postabdomen with epiproct well-developed; spectacles-shaped sclerite typical and well-sclerotised (Fig. 132); spermathecae disc- or tyre-shaped . . . . . *Pullimosina* Roháček

56. Wing vein R_{4+5} distinctly sinuate (basally convex); cell *dm* with rounded posterior outer corner; alula large, apex rounded; male terminalia with epandrium with long dorsolateral seta; larger species (body length: *ca* 1.8–2.4 mm) . . . . . *Terrilimosina* Roháček

– Wing vein R_{4+5} not sinuate (*e.g.*, Figs 45, 46); cell *dm* not rounded; alula small, narrow, or pointed (*e.g.*, Figs 45, 46); male terminalia with epandrium without long dorsolateral seta; smaller species (body length: *ca* 1–1.6 mm). 57

57. Usually larger species (body length: 0.8–1.6 mm); wing vein R_{4+5} slightly bent up to costal vein (*C*), or in some species very slightly sinuate (*e.g.*, Figs 45, 46); antennal scape with medial seta indistinct; thorax with 1 or 2 katepisternal setae, although anterior small; abdominal sternite 5 with posteromedial structure convex or forming appendage; male sternites 6 and 7 normal; male terminalia with surstylus with strong spines (if any) never on apex (Fig. 92); distiphallus variously formed, but usually longer than high. . . . . *Minilimosina* Roháček *sensu lato* 58

– Very small species (body length: 1.1–1.15 mm); wing vein R_{4+5} distinctly bent up to costal vein (*C*); antennal scape with medial seta as long as pedicel; thorax with 1 (posterior) katepisternal seta; male sternite 5 with posteromedial structure concave; male sternites 6 and 7 very weak (Fig. 76); male terminalia with surstylus with strong apical spine (Fig. 110); distiphallus globular, as high as long . . . . . *Oligochaetosella* L. Papp

58. Thorax with 2 dorsocentral setae; acrostichal setae arranged in 4–6 rows of micro-setae between anterior dorsocentral seta; abdominal tergite 1 + 2 longer than tergites 3 and 4 combined; preabdominal sternites with setosity normal, tergites sparsely so, but long pale setose; male terminalia with surstylus usually longer than wide, lobe-shaped or bilobed, usually with thick spines and some projections; female sternite 8 large and broad (Fig. 126) . . . . . *Minilimosina* (*Svarciella* Roháček)

– Thorax with 1 dorsocentral seta in prescutellar position; acrostichal setae arranged in 6 or more rows of micro-setae in front of suture; abdominal tergite 1 + 2 shorter than tergites 3 and 4 combined; both preabdominal sternites and tergites sparsely and shortly setulose; male terminalia with surstylus flat, shorter than wide, with internal processes and keels; female sternite 8 reduced to narrow sclerite or broken into small parts (*e.g.*, Fig. 130) or wholly absent 59

59. Wing cell *dm* present and long, with anterior outer corner acutely angled to rectangular or rarely obtuse angled, its posterior outer corner never acutely angled; wing with costal index (Cs_2 /= R_1 to R_{2+3}/ : Cs_3/= R_{2+3} to R_{4+5}) usually > 0.70; male mid femur with row of basal curved setae ventrally; male terminalia with hypandrial apodeme of medium length; surstylus with robust posterior spine (Fig. 102); basiphallus short, compact; female sternite 8 (Fig. 130) reduced to narrow, elongate sclerite (sometimes divided

into additional small sclerites); larger species (body length: 1.3–1.6 mm) . . . . . *Minilimosina* (*Minilimosina* Roháček)

– Wing cell *dm* short or absent (e.g., Figs 45, 46); wing with costal index invariably < 0.70; male mid femur ventrobasally uniformly setulose; male terminalia with medial apodeme of hypandrium very short (small); surstylus, basiphallus and female sternite 8 not as described above; very small species (body length: 0.80–1.25 mm) 60

60. Wing cell *dm* short, with anterior outer corner obtuse angled and posterior outer corner acute angled and vein M_1 in cell *dm* distinct (Fig. 46); male terminalia with surstylus flat, usually with only 2 lobes; basiphallus longer and more slender; female abdominal sternite 8 reduced to small, short sclerite or absent . . . . . *Minilimosina* (*Allolimosina* Roháček)

– Wing cell *dm* absent; vein M_1 virtually missing (Fig. 45); male terminalia with surstylus not flattened, with several lobes; basiphallus short and compact; female sternite 8 absent . . . . . *Minilimosina* (*Amediella* L. Papp)

61. Wing with first costal sector (basicosta to vein R_1) with some extremely long setae (Fig. 18); membrane with pale brownish clouding (Fig. 18); head with 1 large fronto-orbital seta and 1 large medial interfrontal seta, other cephalic setae weak; mid tibia with mid anteroventral seta and several anterodorsal and posterodorsal setae (Fig. 18); male sternites 3 and 4 with pair of extremely long setae (Fig. 78); male sternite 5 with very thick, long spines (Fig. 67) . . . . . *Acuminiseta* Duda

– Wing with first costal sector (basicosta to vein R_1) with short or medium-long setae only; membrane without brown clouding; head with 2 fronto-orbital and several interfrontal setae (usually < 5) present, if one very large, then this inserted far from eye margin; mid tibia with or without mid anteroventral seta; male sternites 3, 4 and 5 without long, paired setae or spines 62

62. Wing vein R_{4+5} straight (e.g., Fig. 49), or apically slightly recurved; short-winged forms with mid tibia with anteroventral seta below middle (e.g., Fig. 61) 63

– Wing vein R_{4+5} sinuate, or apically bent up to costal vein (C) (fully winged forms); brachypterous forms with R_{4+5} less sinuate and mid tibia without anteroventral seta below middle 65

63. Mid tibia without anteroventral seta below middle (both sexes), in male with long row of short ventral spinules (Fig. 62); male terminalia with surstylus without robust ventral spine; spectacles-shaped sclerite very large, with long, tongue-shaped projection (Fig. 133) (not recorded from Afrotropical Region) . . . . . [*Eulimosina* Roháček]

– Mid tibia with only anteroventral seta below middle in both sexes; male terminalia with surstylus (e.g., Figs 93, 94) with robust ventral spine; spectacles-shaped sclerite normal 64

64. Thorax with 3 dorsocentral setae (anterior two short); wing with alula small and pointed; vein R_{4+5} usually slightly recurved (Fig. 41); male terminalia with surstylus long and narrow (Fig. 93); hypandrial apodeme small; distiphallus highly complex (Fig. 116); female postabdomen with additional small sclerites behind sternite 8 . . . . . *Bifronsina* Roháček

– Thorax with 2 dorsocentral setae; wing with alula large, rounded apically (Fig. 49); vein R_{4+5} never recurved; male terminalia with surstylus short and wide (Fig. 94); hypandrial apodeme long; distiphallus simple; female postabdomen with, at most, 1 additional sclerite behind sternite 8 . . . . . *Spelobia* Spuler [in part]

65. Mid tibia with anteroventral seta below middle; male abdominal sternite 5 with mediocaudal comb of short spines (e.g., Fig. 68), rarely coalesced in sclerotised lamella; female spermathecae tyre- or dish-shaped. 66

– Mid tibia without anteroventral seta below middle; male abdominal sternite 5 with different armature mediocaudally or simple; female spermathecae long cylindrical, vesiculate or subspherical 68

66. Wing vein R_{4+5} apically slightly upcurved to costal vein (C) (Fig. 49); male terminalia with epandrium with fine, long setae; surstylus simple, with 1 robust ventral spine (Fig. 94); female abdominal sternite 8 simple; spermathecae tyre-shaped. . . . . *Spelobia* Spuler [in part]

– Wing vein R_{4+5} very strongly arched up to costal vein (C) (e.g., Fig. 50); other characters not in above combination 67

67. Male terminalia with epandrium without robust spine-like setae; base of postgonite connected to phallapodeme by extremely long, hairpin-like flexible black connections (appearing as second phallapodeme, in profile) (Fig. 99); surstylus simple; basiphallus large, greatly enlarged ventrally, with recurved ventral process; female postabdomen with sternite 8 without projections; spermathecal ducts with sclerotised parts short and bulbous distally; spermathecae various, but not dish-shaped . . . . . *Biphallapodema* L. Papp

– Male terminalia with epandrium with several robust spine-like setae; postgonite to phallapodeme connection simple; surstylus with external and internal lobes; basiphallus small, not greatly enlarged ventrally; female postabdomen with sternite 8 complex, with posterior projections; spermathecal ducts with sclerotised parts short, but not dilated distally; spermathecae dish-shaped . . . . . *Spinilimosina* Roháček *sensu stricto* [in part]

68. Male terminalia with basiphallus with very long pre-epiphallus, but also epiphallus long (Fig. 117); surstylus undivided, compact, with ventral (and also apical) parts with structure composed of minute tubules (Papp 2014*a*, fig. 99); cerci not meeting medially; hypandrium without ventral process; male abdominal sternite 5 without outgoing process, simple, with some short setae only; synsternite 6 + 8 with right-sided sclerite unusually large; spermathecae long cylindrical. . . . . *Preepiphallus* L. Papp

– Male terminalia with basiphallus without epiphallus or pre-epiphallus, but basiphallus may be extremely large and extended ventrally; surstylus without structure composed of minute tubules; synsternite 6 + 8 without enlarged right-sided sclerite; spermathecae ovoid, more or less globular; other characters not in above combination 69

69. Head with frons usually with velvety black (or dark brown) M-shaped mark (Fig. 26); male sternite 5 simple, without mediocaudal armature; male terminalia with hypandrium with large ventral, sometimes bifurcate appendage (Fig. 107); surstylus short, without robust ventral spines (Fig. 95); basiphallus short . . . . . .*Paralimosina* L. Papp [in part]

– Head with frons without velvety M-shaped mark; male sternite 5 with or without mediocaudal lobe; male terminalia with hypandrium not as above, lacking ventral appendage; surstylus with robust ventral spines; basiphallus longer to large 70

70. Male sternite 5 without mediocaudal lobe, but with deeply concave hollow (Fig. 69); hind tibia with 4 or 5 pairs of dorsal setae; male sternite 8 large; male terminalia with cerci not meeting medially; hypandrium with lateral arms fused to epandrium, but not entirely fused to middle apodeme; surstylus and cercus very large, buckle-shaped; surstylus without 2 robust ventral spines; basiphallus large (Fig. 118), extended posteroventrally; female spermathecae ovoid . . . . . *Afrolimosina* L. Papp

– Male sternite 5 with mediocaudal tab-like lobe with groups of spines preceding it (Fig. 70); hind tibia without dorsal setae; male terminalia with cerci meeting below anal fissure; hypandrium not fused to epandrium; surstylus bilobed, with 2 (anterior and posterior) groups of robust ventral spines (Fig. 96); basiphallus compact ventrally, not enlarged; spermathecae more or less globular . . . . . .*Aptilotus* Mik

71. Wing vein R_{2+3} sharply bent apically, sometimes with short appendage (vein R_3); cell *cua* partly closed by incomplete pale vein *CuA*; wings mottled or with dark maculae (Figs 17, 48); legs variegated, sometimes with some tarsal segments white (Fig. 4); thorax usually variegated, with pale micro-tomentose maculae; male terminalia with phallus with thread-like central process . . . . . .*Poecilosomella* Duda

– Wing vein R_{2+3} usually less strongly bent, invariably without short vein appendage; vein *CuA* usually not developed; male terminalia with phallus without long thread-like process; other characters not as described above [some species of *Paralimosina* may also run to here, see notes under "Identification above"] 72

72. Wing evenly darkened, only cell r_1, crossveins and distal part of cell *dm* darker brown; setae on costal vein (*C*) relatively short; male terminalia with epandrium with pair of long anteriorly directed ventral processes (Fig. 89) . . . . . .*Phthitia* (*Rufolimosina* L. Papp)

– Wing pattern usually more extensive; setae on costal vein (*C*) basally to apex of vein R_1 various, but mostly long; male terminalia with epandrium without large, anteriorly directed ventral processes. 73

73. Fore tarsomeres 2–5 white; abdominal sternites 3 and 4 broader than tergites 3 and 4; male sternite 5 as long as broad, with very long setae; male terminalia with surstylus very large and bilobed; distiphallus with forked, soft dorsal process and upcurving ventral process (Papp 1990, figs 23–28) . . . . . Undescribed genus

– Fore tarsomeres 2–5 never white; other characters not as described above 74

74. Head with inner and outer occipital setae very strong, at least as long as anterior fronto-orbital seta; wing membrane (Fig. 19) with dark macula virtually closing cell *cua*; second costal sector (veins R_1 to R_{2+3}) as long as third sector (veins R_{2+3} to R_{4+5}); male terminalia with ventral part of epandrium with 2 pairs of strong thick spines (Fig. 122); male sternite 5 with deep incision mediocaudally; hypandrium without medial part, only 2 lateral arms present (Fig. 108) . . . . . .*Giraffimyiella* L. Papp

– Head with inner and outer occipital setae much weaker, clearly shorter than anterior fronto-orbital seta; wing membrane pattern not as described above; second costal sector (veins R_1 to R_{2+3}) shorter than third sector (veins R_{2+3} to R_{4+5}) (e.g., Figs 40, 47); male terminalia not as described above 75

75. Wing vein R_{2+3} regularly arched up to costal vein (C) (Fig. 40); costal vein (C) with very short setae; costal vein ending far beyond apex of vein R_{4+5}; male abdominal tergite 5 reduced to small sclerite on right side (Fig. 80); male sternite 5 with extremely thick spines centrally (Fig. 71); male terminalia with postgonite simple, bare; surstylus without spiniform setae . . . . . *Afropterogramma* L. Papp

– Wing vein R_{2+3} oblique, virtually straight, with apical part bent perpendicular to costal vein (C) (Fig. 47); costal vein (C) with longer setae throughout its length, costal vein ending at apex of vein R_{4+5}; male abdominal tergite 5 normal, not reduced; male sternite 5 strongly asymmetrical, posteromedially densely and finely setulose; male terminalia with postgonite with numerous setae (Fig. 100); surstylus (Fig. 91) with numerous thick spiniform setae . . . . . *Parapoecilosomella* L. Papp

76. Wings reduced, more or less racket-shaped, oval to scale-like; thorax with prosternum always linear 77

– Wings absent, if remnants of wings present, then these linear (or at least much longer then broad), pointed or narrow and fan-shaped; thorax with prosternum usually broad, but sometimes linear 78

77. Wing rudiment racket-shaped in male, in some species minute oval, without venation; wing scale-like in female; halteres absent or only present as minute sessile pads; abdominal setae long and prominent; head with or without postocellar setae . . . . . *Aluligera* Richards [in part]

– Wing racket-shaped, with costal vein (C) and veins R_{2+3} and R_{4+5} distinct; halteres virtually normal, only slightly reduced; abdomen without long setae; head without postocellar setae . . . . . *Kabaria* Richards

78. Head with ocelli 79

– Head without ocelli 88

79. Scutellum short, not semicircular, with long apical and very much shorter basal scutellar setae; thorax with prosternum broad; abdomen without long outstanding setae; head with 2 pairs of fronto-orbital setae; postocellar setae absent . . . . . *Scutelliseta* Richards

– Scutellum long, often semicircular, with all scutellar setae long, *i*.e., basal setae not as described above; other characters not in above combination 80

80. Thorax with 2 pairs of dorsocentral setae (e.g., Fig. 23); prosternum linear; abdomen with long outstanding setae [*Ocellusia* may also run to here and is not keyed further, see "Identification" above] 81

– Thorax with 1 or 3 pairs of postsutural dorsocentral setae; prosternum variously developed; abdomen mostly without long outstanding setae (except in some *Aluligera*, formerly in *Uluguria* Richards) 84

81. Very small flies (body length: 1.0–1.1 mm); thorax and abdomen strongly convex (Fig. 23); wing greatly reduced in form of closed fan (Fig. 23) . . . . . *Reunionia* L. Papp

– Mostly larger flies (body length > 1.1 mm); thorax and abdomen less convex; wing rudiment (if present) different in shape 82

82. Head without postocellar setae; mid tibia with paired setae at $\frac{1}{3}$ and $\frac{3}{4}$ of length; male terminalia with surstylus complex, with 3 complicated lobes, bearing robust, black tooth-like setae . . . . . *Paraptilotus* Richards [in part]

– Head often with postocellar setae; mid tibia differently setose; male terminalia with surstylus simple, with setose basal lobe and more or less long process, but without tooth-like setae 83

83. Scutellum semicircular; wing rudiments racket-shaped (males) or absent (females of most species) and halteres sometimes present although reduced; head with 2 pairs of fronto-orbital setae; mid tibial setae various; male terminalia with surstylar process asymmetrical and finely pointed; cerci with shorter setae . . . . . *Aluligera* Richards [in part]

– Scutellum shorter than semicircular; wings and halteres absent; head with 3 pairs of fronto-orbital setae; mid tibia with pair of setae at $\frac{1}{3}$ and 1 anterodorsal, 1 dorsal and 1 posterodorsal seta at $\frac{4}{5}$ length; male terminalia with surstylar process widened apically; cercus with pair of extremely long setae. . . . . *Trisetomyia* Richards

84. Scutellum strongly transverse, with hind margin virtually straight; thorax with prosternum rather wide; abdomen 2.5 × as wide as thorax . . . . . *Lobeliomyia* Richards

– Scutellum more or less semicircular, with hind margin rounded; thorax with prosternum variable; abdomen at most 2 × as wide as thorax 85

85. Scutellum with basal seta inserted somewhat on disc, apical scutellar seta very small or absent; mid tibia with unpaired setae at $\frac{1}{3}$ and $\frac{4}{5}$ length . . . . . *Aluligera* Richards [in part]

– Scutellum with basal seta marginal, apical scutellar seta long; mid tibia with basal and distal paired setae 86

86. Head with 1–2 pairs of fronto-orbital setae; frons usually with M-shaped mark (Fig. 26); male terminalia with hypandrium with robust bifurcate ventral process; surstylus short, bilobed [in all probability *Gobersa* de Coninck also keys here; this proposal is tentative; a study of male terminalia would be necessary for a final decision] . . . . . .*Paralimosina* L. Papp [in part]

– Head with 2–3 pairs of fronto-orbital setae; frons without M-shaped mark, with or without 3 stripes; male terminalia not as described above 87

87. Thorax with prosternum at least somewhat broadened; head with 3 pairs of fronto-orbital setae (although anterior pair shortened); frons with 3 stripes; 1 pair of dorsocentral setae; abdomen sometimes corrugated; species with concolourous thorax and abdomen (restricted to Central and East African mountains). . . . . *Mesaptilotus* Richards

– Thorax with prosternum linear; head with 2 pairs of fronto-orbital setae; frons without stripes; 3 pairs of dorsocentral setae; abdomen never corrugated; yellow species with black abdomen and dark longitudinal pleural band (restricted to Saint Helena I.). . . . . *Phthitia* (*Phthitia* Enderlein)

88. Abdomen basally with distinct stalk ("petiole"), *i.e.*, basal abdominal segments strongly narrowed (e.g., Fig. 24); abdomen with very long outstanding setae 89

– Abdomen oval or with broad, very short basal stalk ("petiole") (e.g., Fig. 25); abdomen with setae variable 90

89. Abdominal stalk ("petiole") transverse; thorax with prosternum short and broad; head without interfrontal and fronto-orbital setae; mid tibia with distinct apicoventral seta, but with only 1 anterodorsal seta at $^4/_5$ length . . . . . *Oribatomyia* Richards

– Abdominal stalk ("petiole") (formed by tergite 1 + 2), longer than broad (Fig. 24) giving body apterous ant-like appearance; thorax with prosternum linear; head with 3 pairs of interfrontal setae; 0–1 fronto-orbital setae; mid tibia with reduced apicoventral seta, but with unpaired (anterodorsal) setae at $^1/_3$ and $^4/_5$ length . . . . . *Pismira* Richards

90. Abdomen without long outstanding setae (Fig. 25); thorax with 1 dorsocentral seta (Fig. 25); prosternum short and broad; head without fronto-orbital and ocellar setae; scutellum transverse, with very long basal setae, apical scutellar setae minute or absent; mid tibial setae reduced and weak . . . . . *Ocellipsis* Richards

– Abdomen with long outstanding setae; thorax with 2 dorsocentral setae; prosternum linear; head with 2 pairs of fronto-orbital setae and ocellar setae well-developed; scutellum semicircular, with 2 pairs of marginal setae; mid tibial setae paired and rather strong 91

91. Abdomen with raised collar anteriorly; male terminalia with surstylar process asymmetrical and finely pointed distally . . . . . .*Aluligera* Richards [in part]

– Abdomen normal anteriorly; male terminalia with surstylus complex, with 3 complicated lobes, bearing robust, black tooth-like setae . . . . . *Paraptilotus* Richards [in part]

Synopsis of the fauna

The global fauna of Sphaeroceridae comprises > 1,800 described species in 159 genera (Marshall *et al*. 2011 and recent additions), but as most regional faunas are inadequately studied, the actual number may be estimated at > 5,000 species. The Afrotropical fauna currently comprises 411 species (395 in 72 genera, plus 16 unplaced species). The total numbers of known species within genera listed below were obtained by critical revision of data from the World catalog of Sphaeroceridae (Roháček *et al*. 2001), its update (Marshall *et al*. 2011) and subsequent taxonomic additions published from 2012–2020.

The Afrotropical fauna is well-known only as far as coprophagous species are concerned. Terricolous species, particularly those occurring in rainforests, are far less known and the broad concept of "rich savannas, poor rainforest", as postulated by Kirk-Spriggs & Stuckenberg (2009) does not appear to apply to the Sphaeroceridae.

The family is species-rich on all continents (except the high Arctic and Antarctica) and is also represented on subantarctic islands. Some species (*Bifronsina bifrons* (Stenhammar, 1855), *Coproica* (at least five species), *Ischiolepta pusilla* (Fallén, 1820), *Leptocera caenosa* (Rondani, 1880), *Sphaerocera curvipes* Latreille, 1805, *Telomerina flavipes* (Meigen, 1830), *etc.*, chiefly associated with dung of domestic animals, are virtually cosmopolitan, having been spread around the world through human activities. Some coastal species, associated with kelp and other marine algae are similarly widespread, apparently due to overseas shipping, *e.g.*, *Thoracochaeta brachystoma* (Stenhammar, 1855) and *T. zosterae* (Haliday, 1833).

A peculiarity of the Afrotropical sphaerocerid fauna is the high proportion of apterous and reduced-winged genera (see Kirk-Spriggs & Muller 2017: 230, for review). Brachypterous (including micropterous), stenopterous and apterous species are known in 14 genera in the region (13 in the subfamily Limosininae). Those limosinine genera may be grouped according to their distribution ranges: (1) one genus occurring

on a single mountain (six cases); (2) genera more widely distributed on more than one mountain (six cases); (3) genera occurring at low elevations (1 case, the genus *Scutelliseta*); and (4) a single insular species in the large and widespread genus *Phthitia*, with otherwise mostly fully winged species. It is not excluded, however, that some of these wingless genera also include fully winged species and, as their relationships are not adequately known, these could prove to be synonymous with other genera with winged species.

***Achaetothorax* Hedicke** (Copromyzinae)**.** A genus of 18 described species (Fig. 14) occurring in the Afrotropical and Oriental Regions. Sixteen species occur in the Afrotropics, distributed in East, Central and Southern Africa, mainly in the tropical belt, but two species are known from South Africa (Papp 2017). Species are coprophagous and are abundant as part of the dipterous communities of fresh elephant dung and the dung of large-bodied hoofed mammals. The biology and immature stages otherwise remain unknown. For species identification refer to Norrbom & Papp (1994), Papp (2017) and Papp & Norrbom (1992) and an identification key to the majority of known species was provided by Papp & Norrbom (1992).

***Acuminiseta* Duda** (Limosininae)**.** A probable endemic genus (Fig. 18) of three Afrotropical species: *A. ceropteroides* L. Papp, 2008 and *A. rugarii* (Vanschuytbroeck, 1950), described from Democratic Republic of Congo; and the type species of the genus, *A. pallidicornis* (Villeneuve, 1916), recorded from Cameroon, Democratic Republic of Congo and Republic of Congo. Three additional extralimital species recorded from the Australasian and Oriental Regions (Roháček *et al*. 2001: 111), are probably not congeneric and need revision (Papp 2008*b*). *Acuminiseta pallidicornis* is known to be kleptoparasite on giant millipedes, riding on their backs and ovipositing into their droppings (Disney 1975). The immature stages remain unknown. No identification key to Afrotropical species is currently available (see Papp 2008*b*) and placement of *A. rugarii* to *Acuminiseta* remains uncertain (Vanschuytbroeck 1950*b*), pending a revision of the type material.

***Afrolimosina* L. Papp** (Limosininae)**.** An endemic monotypic genus, with the single species, *A. albitarsis* L. Papp, 2014, described from Burundi and Namibia. The biology and immature stages of the species remain unknown, but the type material was sampled using Malaise traps, found in aerial plankton and adults were attracted to light. For species identification refer to Papp (2014*a*).

***Afromyia* Kim** (Sphaerocerinae)**.** An endemic genus of six described species, distributed in East, Central, Southern and West Africa, mainly in the tropical belt from Ghana to Ethiopia, with the most widespread species, *A. wittei* (Vanschuytbroeck, 1948), also known from Lesotho. The biology is poorly known, but adults have been sampled from elephant dung and sifted from a rotten *Raphia* (Arecaceae) palm stem (two species) or were swept in rainforest (Papp 1978). For descriptions and identification keys refer to Kim (1968) and Papp (1978).

***Afropterogramma* L. Papp** (Limosininae)**.** An endemic monotypic genus, with the single species, *A. minor* L. Papp, 2008, described from Tanzania based the unique male holotype. *Afropterogramma minor* is very small species with patterned wings (Fig. 40). The biology and immature stages remain unknown. For the identification of the species refer to Papp (2008*b*).

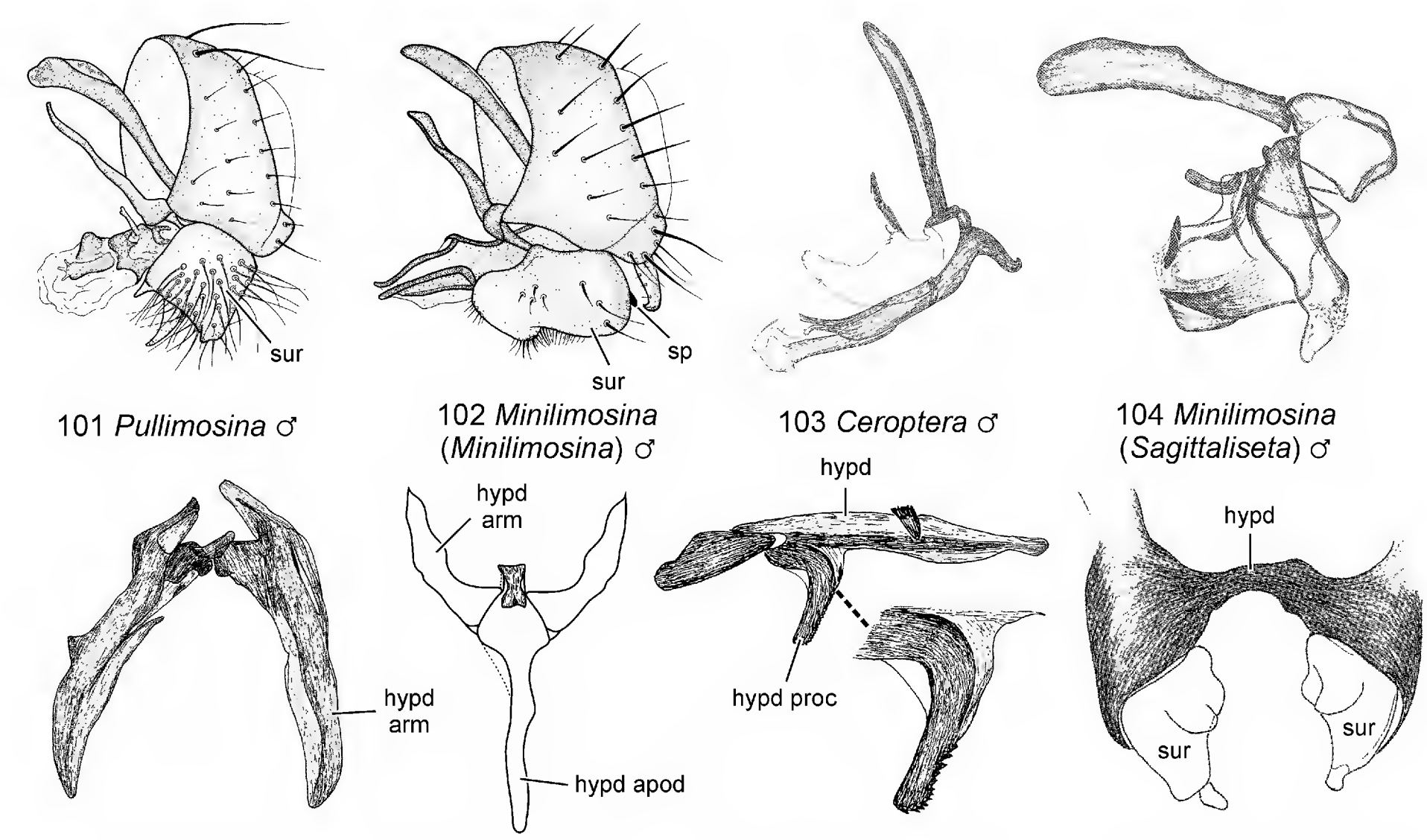
***Aluligera* Richards** (Limosininae). An endemic genus of 20 described species, distributed in Central and East Africa, *i.e*., Democratic Republic of Congo (Kivu), Ethiopia (Simien), Kenya (Mt Elgon), Tanzania (Mt Meru and Uluguru Mountains (Eastern Arc Mountains)) and Uganda (Ruwenzori Mountains). One species, *A. varicolor* (Richards, 1957), is more widely distributed, having been described from Mt Elgon, Kenya, but also reported from Tanzania and Uganda. The latter species, plus three other brachypterous species, were placed in *Aluligera* by Roháček *et al*. (2001: 112). Species with the basal scutellar setae inserted somewhat discally and the apical scutellar setae very small or absent were originally described in the genus *Uluguria* (preoccupied by *Uluguria* Hoffman, see Koçak & Kemal 2009), namely: *A. maculata* (Richards, 1965) and *A. nigra* (Richards, 1965), but were later also transferred to *Aluligera* by Roháček *et al*. (2001: 113). All species of the genus are obviously terricolous, occurring in detritus and humus in various types of montane forests and in moss in *Senecio* forests and type localities are all at high elevations (1,500–4,000 m) (see Richards 1955, 1965, 1966). The immatures remain unknown. Richards (1966) provided an identification key to wingless species, but no identification key is available for other species.

***Anommonia* Schmitz** (Limosininae)**.** An endemic genus with six described species, distributed in East, Central and West Africa. The Oriental species, *A. flavicaput* (Richards, 1968*a*), described from Indonesia, obviously does not belong to this genus (Papp 2008*b*). Species of the genus are of interest, both in terms of the peculiar form of the adult body and in their life habits, occurring in association with driver ants, *Dorylus* (*Anomma* Shuckard) (Hymenoptera: Formicidae). The immature stages remain unknown. An identification key including the six Afrotropical species was provided by Richards (1968*a*).

***Aptilotus* Mik** (Limosininae)**.** A genus of 32 described species, occurring in all zoogeographical regions, except Antarctica. Only one species is recorded from the Afrotropics, the winged *A. carbonicolor* (Richards, 1959), described from Ethiopia, which was transferred to *Aptilotus* by Marshall & Smith (1990). Additional undescribed species should be expected at least in East Africa. The relationships of some apterous Afrotropical genera to *Aptilotus* requires further study. Species of this genus are terricolous and usually occur in leaf litter and other detritus in humid forests (Marshall & Smith 1990). The immature stages remain unknown.

***Archicollinella* Duda** (Limosininae). A genus of three species occurring in the Afrotropical, Neotropical and Palaearctic Regions. The single Afrotropical species, *A. penteseta*, was originally described from specimens collected in the Scilly Is. of Great Britain, but is in fact native to the Namibian guano islands, the type material likely representing an introduction through the guano trade of the 1840s (Kirk-Spriggs 2007). Larvae develop in seabird guano and the carcasses of Cape fur seals, and the immature stages were described and figured by Kirk-Spriggs (2007). Wheeler & Marshall (1991) revised the genus and provided an identification key to the three species.

***Aspinilimosina* L. Papp** (Limosininae)**.** A genus of two species occurring in the Afrotropical and Oriental Regions. The genus was originally described to accommodate the Oriental species *A. postocellaris* L. Papp, 2004, described from Sri Lanka, but the Afrotropical species formerly known as *Ceroptera ndelelensis* Vanschuytbroeck, 1959, described from Democratic Republic of Congo also belongs to this genus (Papp 1914*b*). Several undescribed species are known from the Oriental Region



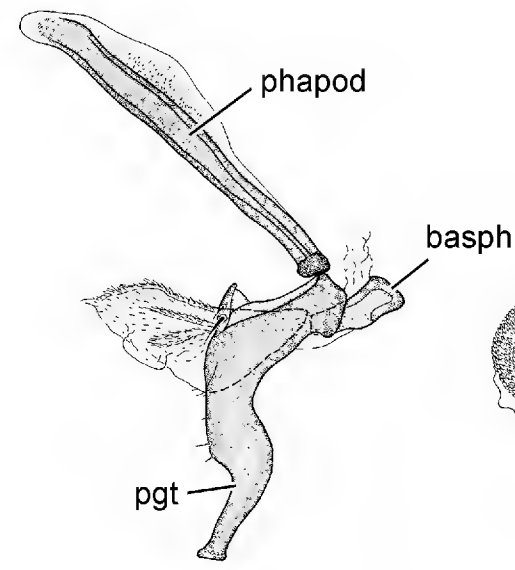
101 *Pullimosina* ♂ 102 *Minilimosina* (*Minilimosina*) ♂ 103 *Ceroptera* ♂ 104 *Minilimosina* (*Sagittaliseta*) ♂

105 *Dudaia* ♂ 106 *Norrbomia* ♂ 107 *Paralimosina* ♂ 108 *Giraffimyiella* ♂

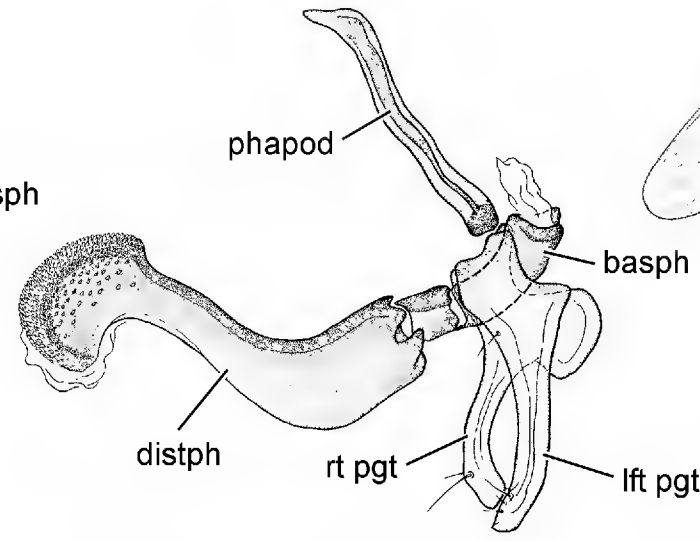
109 *Eximilimosina* ♂ 110 *Oligochaetosella* ♂ 111 *Norrbomia* ♂

Figs 99.101–111. Male terminalia of Sphaeroceridae: (101) *Pullimosina moesta* (Villeneuve), lateral view (non-Afrotropical); (102) same, *Minilimosina* (*Minilimosina*) *parvula* (Stenhammar); (103) phallic complex of *Ceroptera rufitarsis* (Meigen), lateral view (non-Afrotropical); (104) same, *M.* (*Sagittaliseta*) *siamensis* L. Papp (non-Afrotropical); (105) hypandrium of *Dudaia flavocincta* (Duda), ventral view; (106) same, *Norrbomia spinosa* (Vanschuytbroeck); (107) same, *Paralimosina flavifacies* L. Papp, lateral view; (108) hypandrium and surstyli of *Giraffimyiella giraffa* (Richards), ventral view; (109) surstylus of *Eximilimosina thailandica* L. Papp, sublateral (widest extension) view (non-Afrotropical); (110) same, *Oligochaetosella inconspicua* L. Papp, sublateral (widest extension) view; (111) cerci of *N. sarcophaga* L. Papp, caudal view. Fig. 101 (Roháček 1985, fig. 748), Fig. 102 (Roháček 1983, fig. 276), Fig. 103 (Papp 2014*b*, fig. 24), Figs 104, 108, 109 (Papp 2008*b*, figs 163, 92, 56, respectively), Fig. 105 (Papp & Norrbom 2015, fig. 11 © Magnolia Press), Figs 106, 111 (Papp 1988, figs 35, 26, respectively), Fig. 107 (Papp 2013, fig. 6), Fig. 110 (Papp 2014*a*, fig. 66 © Magnolia Press).

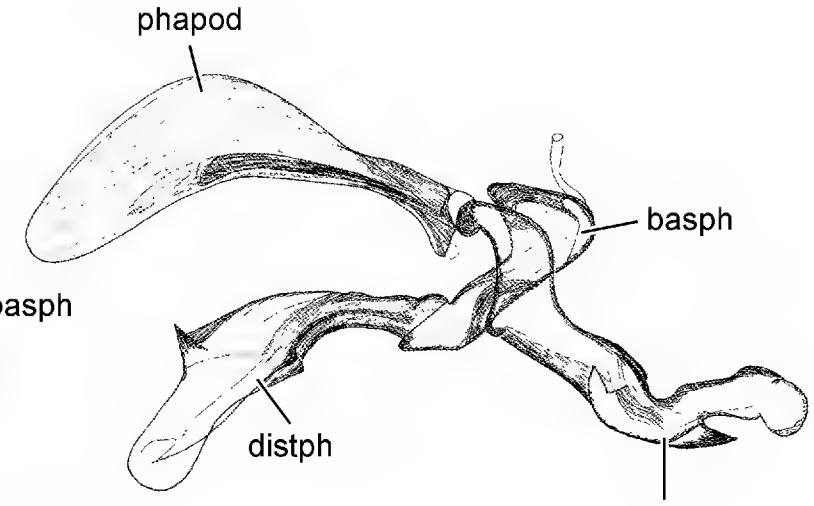
Abbreviations: cerc – cercus; hypd – hypandrium; hypd apod – hypandrial apodeme; hypd arm – hypandrial arm; hypd proc – hypandrial process; sp – spine; sur – surstylus.



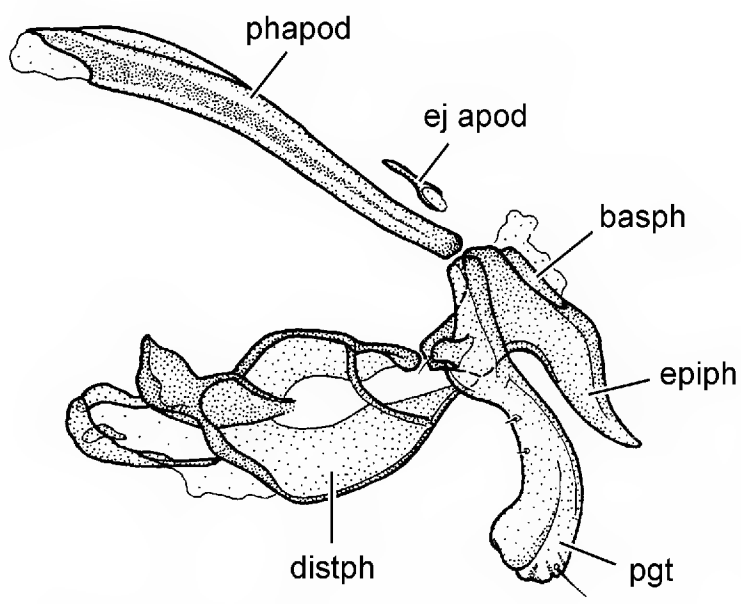
112 *Pseudocollinella* ♂



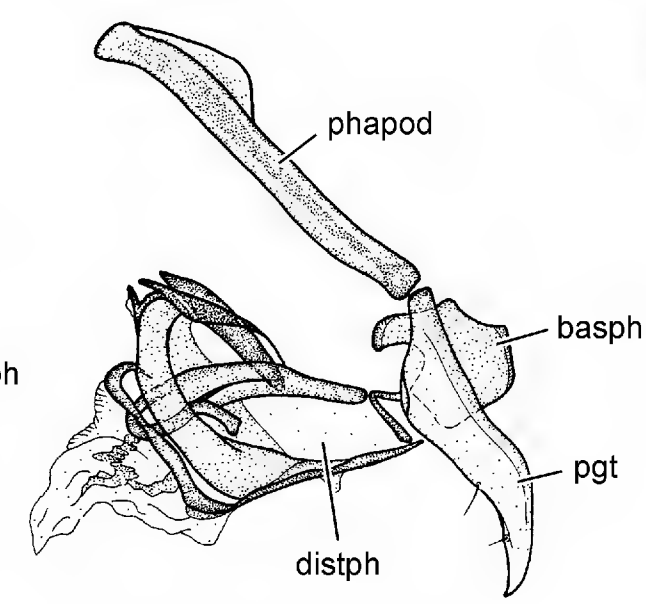
113 *Puncticorpus* ♂



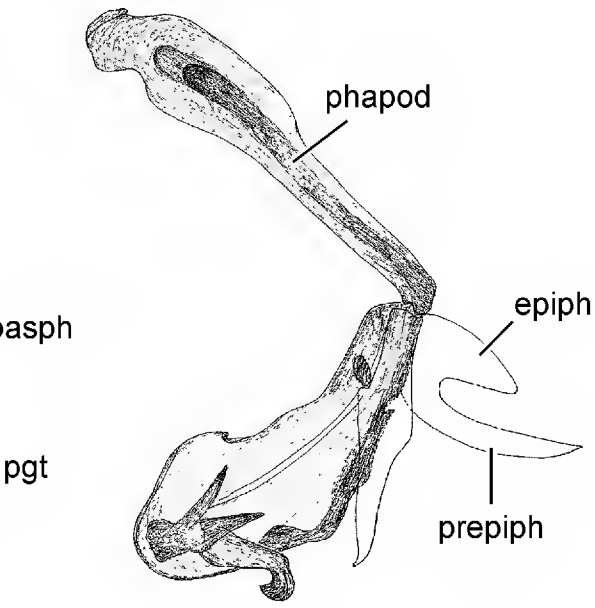
114 *Setositibiella* ♂



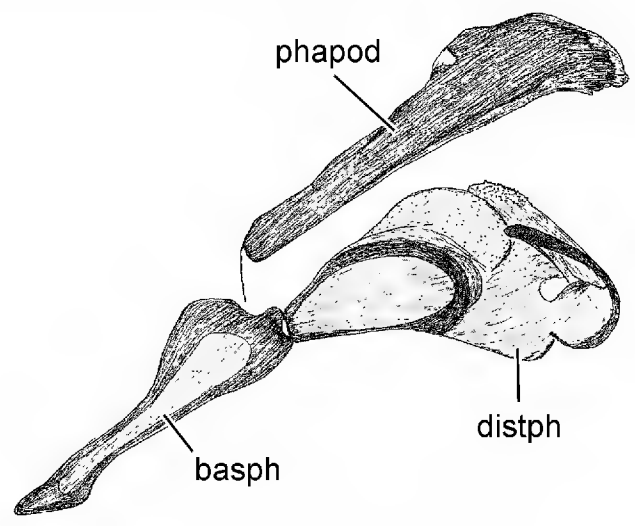
115 *Opalimosina* (*Opalimosina*) ♂



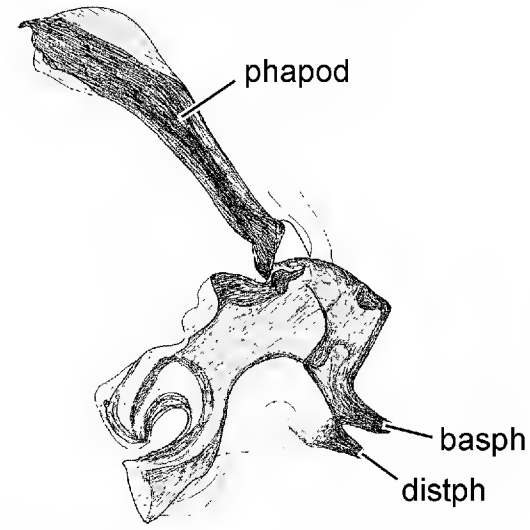
116 *Bifronsina* ♂



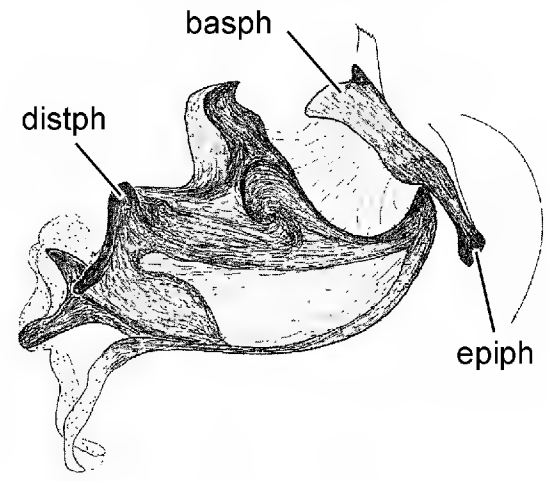
117 *Preepiphallus* ♂



118 *Afrolimosina* ♂



119 *Subacuminiseta* ♂



120 *Chelilimosina* ♂

Figs 99.112–120. Male terminalia of Sphaeroceridae: (112) phallic complex of *Pseudocollinella abhorrens* (Roháček), lateral view (non-Afrotropical); (113) same, *Puncticorpus cribratum* (Villeneuve) (non-Afrotropical); (114) same, *Setositibiella terrestris* L. Papp; (115) same, *Opalimosina* (*Opalimosina*) *collini* (Richards) (non-Afrotropical); (116) same, *Bifronsina bifrons* (Stenhammar); (117) same, *Preepiphallus endrodyi* L. Papp; (118) phallus and phallapodeme of *Afrolimosina albitarsis* L. Papp, lateral view; (119) same, *Subacuminiseta minor* L. Papp, lateral view; (120) phallus of *Chelilimosina baloghi* L. Papp, lateral view. Figs 112, 113 (Roháček 1998, figs 104, 42, respectively), Fig. 114 (Papp 2008*b*, fig. 291), Figs 115, 116 (Roháček 1985, figs 1065, 696, respectively), Figs 117–120 (Papp 2014*a*, figs 90, 6, 113, 44, respectively © Magnolia Press).

Abbreviations: basph – basiphallus; distph – distiphallus; ej apod – ejaculatory apodeme; epiph – epiphallus; lft pgt – left postgonite; pgt – postgonite; phapod – phallapodeme; prepiph – pre-epiphallus; rt pgt – right postgonite.

(Papp 2008*b*), but none from the Afrotropics. The biology and immature stages remain unknown. For a re-description of *A. ndelelensis* and synonymy refer to Papp (2014*b*).

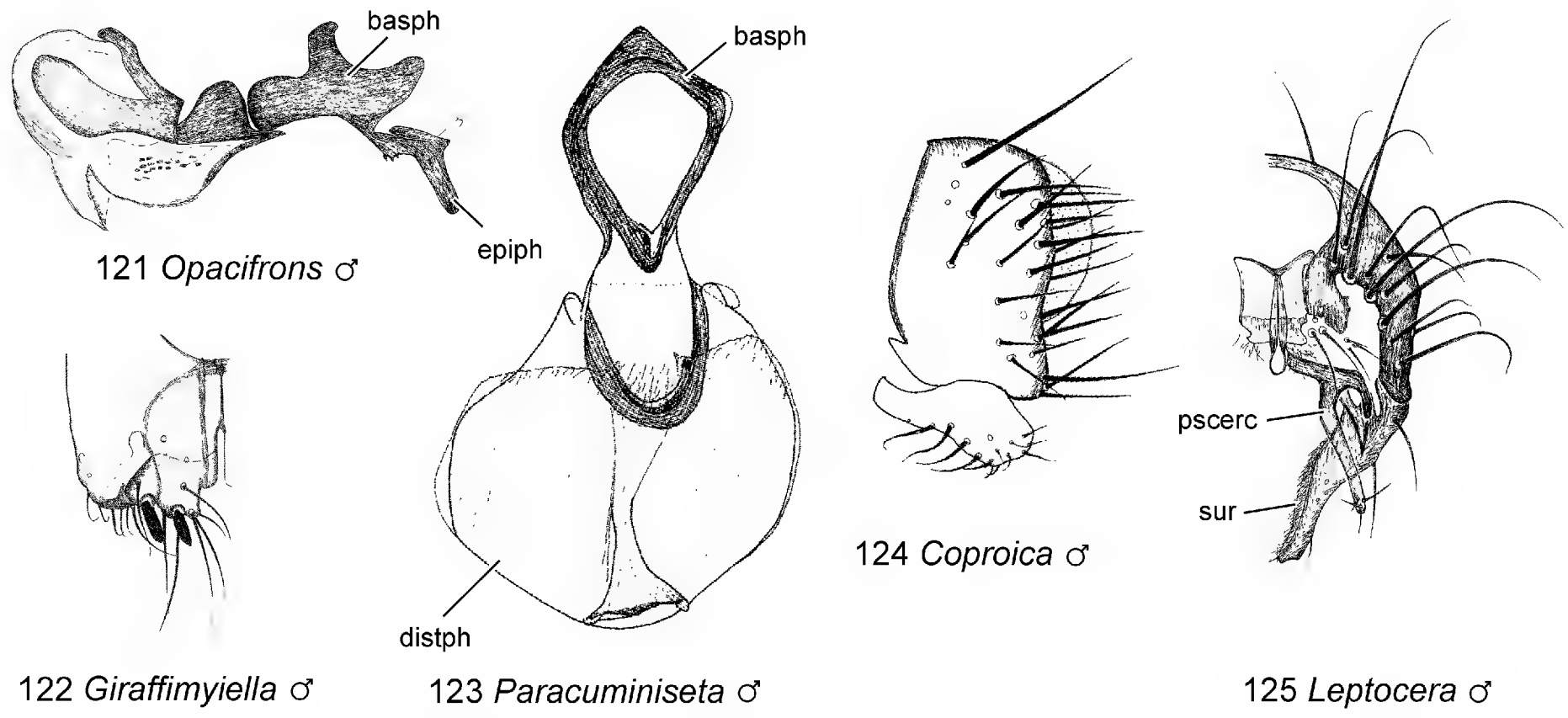
***Bifronsina* Roháček** (Limosininae)**.** A genus of five described species occurring in the Afrotropical, Oriental and Palaearctic Regions (Marshall *et al*. 2011). Three species occur in the Afrotropics: the type species *B. bifrons*, recorded from Democratic Republic of Congo, Madagascar, Seychelles, South Africa and United Arab Emirates; *B. latitarsis* L. Papp, 2008, from Kenya, Nigeria and Tanzania; and *B. nigroscutellata* (Duda, 1925), described from Ethiopia (Papp 2008*b*). *Bifronsina* species are saprophagous (primarily coprophagous) and often occur on elephant and buffalo dung in the Afrotropics. The egg and puparium of *B. bifrons* were described by Okely (1974) and the egg by Tenorio (1968). Papp (2008*b*) provided an identification key to all described species.

***Biphallapodema* L. Papp** (Limosininae)**.** An endemic genus of two described species: *B. oligodentata* L. Papp, 2014 and *B. polydentata* L. Papp, 2014, both described from Republic of Congo. *Biphallapodema* are small flies, with peculiar male terminalia and the body is not strongly sclerotised and not granulose. The genus appears to be terricolous and all known species were collected by means of pitfall traps. The biology and immature stages otherwise remain unknown. For descriptions of the two species refer to Papp (1914*a*).

***Ceroptera* Macquart** (Limosininae)**.** A genus of 29 species (Figs 16, 20, 21), occurring in the Afrotropical, Nearctic, Oriental and Palaearctic Regions, being particularly rich in subtropical and tropical parts of the Old World (Papp 1977). A recent revision raised the number of the Afrotropical species to 20, distributed in East, Central, Southern and West Africa, the Atlantic and Indian Ocean Islands and the Southern Arabian Peninsula (Papp 2014*b*). Two species formerly assigned to *Ceroptera* have now been transferred to other genera, namely *C. ealensis* Vanschuytbroeck, 1951, transferred to *Mislocatus* (Papp 2008*b*, 2014*a*) and *C. ndelelensis* to *Aspinilimosina* (see above). *Ceroptera* species are probably all commensal (kleptoparasitic) on dung beetles (Coleoptera: Scarabaeidae), with adult flies attaching themselves, usually to the undersides of adult beetles for most of their adult life (Fig. 7), with females ovipositing into dung balls prepared and buried by them. Consequently, larvae develop in dung underground, protected against enemies. The immature stages remain unknown. An identification key to Old World species (including the 20 Afrotropical species) was provided by Papp (2014*b*).

***Ceropterella* Richards** (Limosininae)**.** An endemic genus of two described species: *C. mirifica* L. Papp, 2017 (Fig. 22), described from Namibia; and *C. nitidosa* (Richards, 1953), reported from Mozambique, Republic of Congo and South Africa. In addition to the key characters noted above, *Ceropterella* is distinguished by the complete fusion of the basiphallus and distiphallus (Papp 2017), resembling the genus *Thoracochaeta*. The type specimens of *C. nitidosa* were collected off the dung beetle *Pachylomera femoralis* Kirby (Scarabaeidae) in April 1951 (Richards 1953), but the immature stages remain unknown. For descriptions and identification of both described species refer to Papp (2017).

***Chaetopodella* Duda** (Limosininae)**.** An Old World genus of 13 described species occurring in the Afrotropical, Oriental

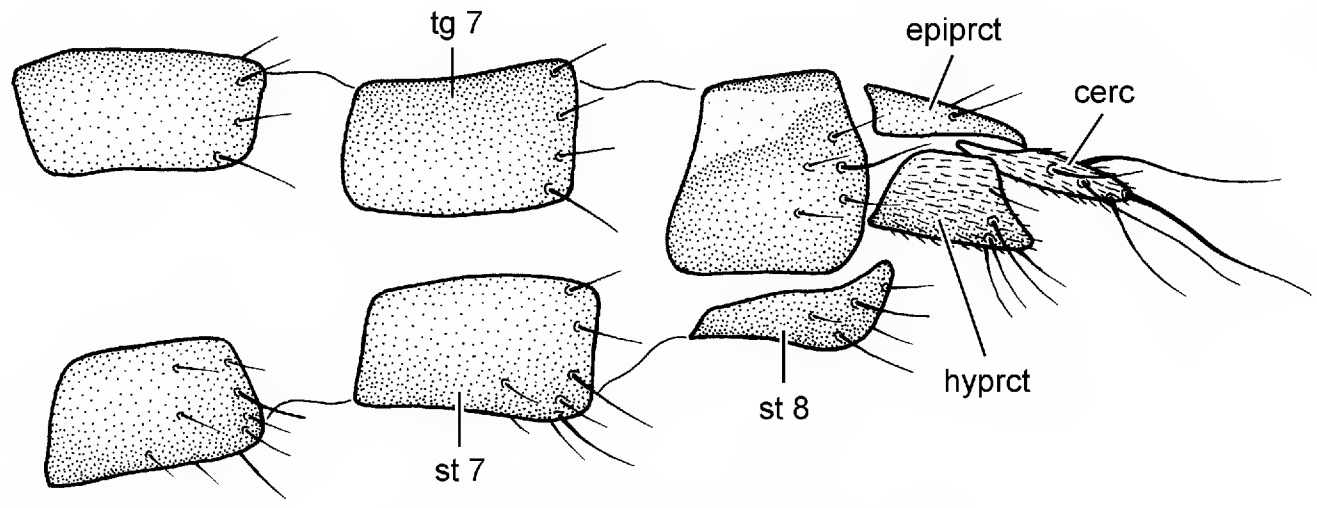


Figs 99.121–125. Male terminalia of Sphaeroceridae: (121) phallus of *Opacifrons subserra* L. Papp, lateral view; (122) left half of ventral part of epandrium of *Giraffimyiella giraffa* (Richards), caudal view; (123) phallus of *Paracuminiseta tetraspinosa* L. Papp, ventral view; (124) epandrium, surstylus and anal plate of *Coproica demeteri* L. Papp, lateral view; (125) right half of terminalia of *Leptocera marginata* (Adams), caudal view. Fig. 121 (Papp 2012*a*, fig. 38), Figs 122, 123 (Papp 2008*b*, figs 89, 204), Fig. 124 (Papp 2008*a*, fig. 7), Fig. 125 (Papp 2012*b*, fig. 54).

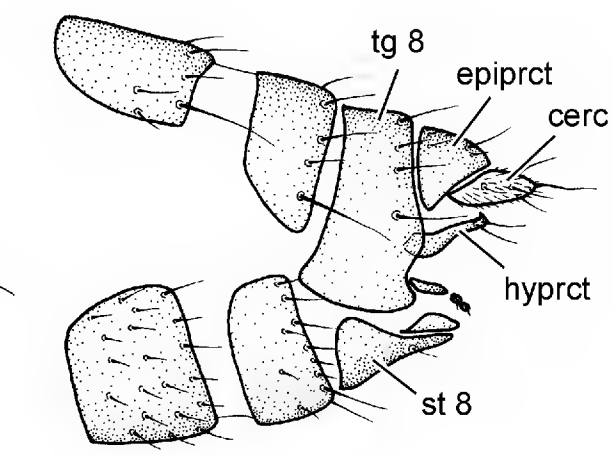
Abbreviations: basph – basiphallus; distph – distiphallus; epiph – epiphallus; pscerc – pseudocercus; sur – surstylus.

and Palaearctic Regions (Hayashi & Papp 2007; Papp 2008*c*). Eight species occur in the Afrotropics, distributed in Central, East, Southern and West Africa. The genus is divided into two subgenera: *Chaetopodella sensu stricto* (with six Afrotropical species) and *C.* (*Afrochaetopodella* L. Papp), endemic to Afrotropics, with two species: *C.* (*A.*) *keniaca* L. Papp, 2008 and *C.* (*A.*) *reducta* L. Papp, 2008. The subgenus *C.* (*Afrochaetopodella*) differs from *Chaetopodella sensu stricto* as follows: all inter-frontal setae are short, the anterior fronto-orbital seta is reduced, the setae on the first costal sector (from basicosta to vein R_1) are short, much shorter than the width of the costal cell (*c*), the male preabdomen is very long and slender, male sternite 5 has a pair of trilobed caudal processes, the subepandrial sclerite is without strong thorn-like setae and the male terminalia are small, with the postgonite robust, with several edges or tips. *Chaetopodella* species are saprophagous (chiefly coprophagous) and larvae mainly develop in dung. Immature stages of the extralimital species *C. scutellaris* (Haliday, 1836), including the egg and larva, were described by Lachmann (1991) and Schumann (1961, 1962). Afrotropical species were described and an identification key provided by Papp (2008*c*).

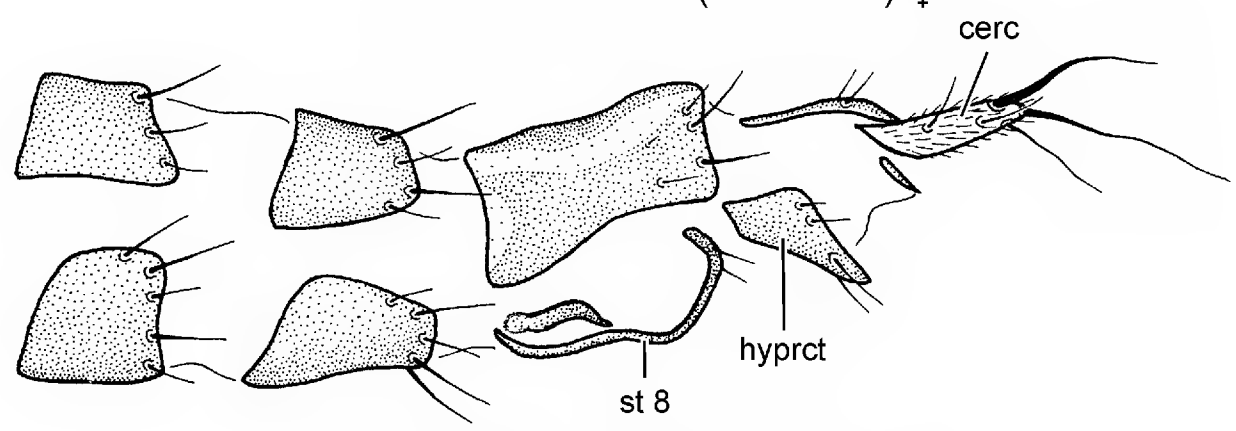
***Chaetosifemur* L. Papp** (Limosininae)**.** An endemic monotypic genus, with the single species, *C. longiventre* L. Papp,



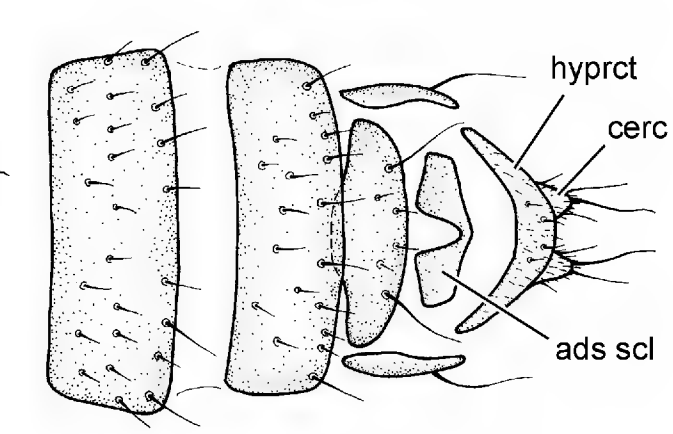
126 *Minilimosina* (*Svarciella*) ♀



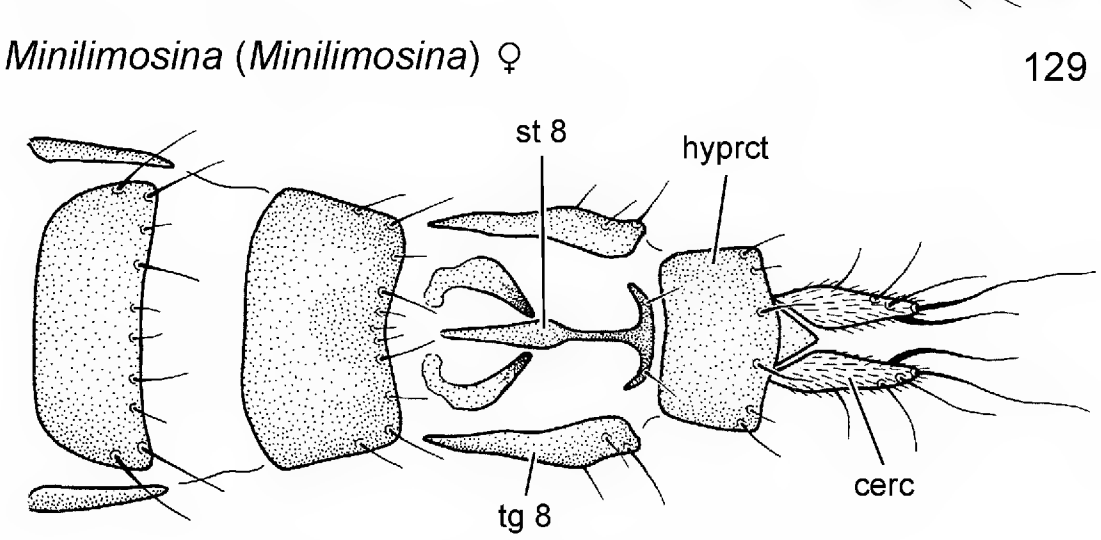
127 *Bifronsina* ♀



128 *Minilimosina* (*Minilimosina*) ♀



129 *Pullimosina* ♀



130 *Minilimosina* (*Minilimosina*) ♀

Figs 99.126–130. Female postabdomens of Sphaeroceridae: (126) *Minilimosina* (*Svarciella*) *vitripennis* (Zetterstedt), lateral view (non-Afrotropical); (127) same, *Bifronsina bifrons* (Stenhammar), lateral view; (128) same, *M.* (*Minilimosina*) *parvula* (Stenhammar) (non-Afrotropical); (129) *Pullimosina moesta* (Villeneuve), ventral view (non-Afrotropical); (130) same, *M.* (*M.*) *parvula* (non-Afrotropical). Fig. 126 (Roháček 1982, fig. 189), Figs 127, 129 (Roháček 1985, figs 702, 753), Figs 128, 130 (Roháček 1983, figs 281, 282).

Abbreviations: ads scl – additional sclerite; cerc – cercus; epiprct – epiproct; hyprct – hypoproct; sg – segment; st – sternite; tg – tergite.

2008, described from Tanzania. *Chaetosifemur* is one of the genera in which the abdominal tergites are de-sclerotised, with extremely long tergal setae. The male terminalia have the basiphallus and distiphallus fused, but with the boundary faintly visible, the distiphallus is heavily sclerotised, bearing a long backwardly directed process and the basiphallus has a large epiphallus (Papp 2008*b*). The type material was collected by netting over elephant dung in Tanzania. The immature stages remain unknown.

***Chelilimosina* L. Papp** (Limosininae)**.** An endemic monotypic genus, with the single described species, *C. baloghi* L. Papp, 2014, described from Democratic Republic of Congo. A very small species, with the wing length only slightly greater than 1.0 mm. The body is less sclerotised and not granulose, but the abdominal tergites are well-sclerotised. The male fore tarsus has the outer claw very large (Fig. 58) and the inner claw thin and normally developed. It is probably a terricolous species, as all known specimens were collected in pitfall traps in a forest. The immature stages remain unknown. Papp (2014*a*) provided the original description of the species.

[***Chespiritos* Marshall** (Limosininae)**.** A genus with 21 described species occurring in the Neotropical and Palaearctic Regions (Kuwahara & Marshall 2020), but with only one species, *C. pervadens* Roháček & Buck, 2003, recorded from the Old World. Although the genus is not recorded from the Afrotropical Region, it is included in the above identification key, as *C. pervadens* was introduced into the Canary Is. (Roháček & Buck 2003), making its introduction (and possibly other species of the genus) to the Afrotropics possible. Species of *Chespiritos* appear to be mainly associated with rotting plant matter. The immature stages remain unknown. Species can be identified by reference to Kuwahara & Marshall (2020).]

***Coproica* Rondani** (Limosininae)**.** A genus of 47 described species, occurring in all zoogeographical regions, except Antarctica. Eighteen species occur in the Afrotropical Region, distributed in Central, East, Southern and West Africa, the Indian Ocean Islands and the Southern Arabian Peninsula. Five species, probably of Afrotropical origin, have become virtually cosmopolitan through human activity (mainly animal husbandry) and 13 other species are endemic to the Afrotropics and were described by Papp (2008*a*, 2015). Several additional undescribed species should be expected from the region. *Coproica* species are typically coprophagous, associated with dung of larger mammals, but some are more widely saprophagous and occur on decaying organic matter of various types, including carrion, fungi and decaying plant material. Immature stages have been described for extralimital species (egg, larva and puparium) by Goddard (1938), Lachmann (1991), Laurence (1955), Okely (1974) and Schumann (1961, 1962). Afrotropical *Coproica* species can be identified by reference to Papp (2008*a*, 2015).

***Copromyza* Fallén** (Copromyzinae)**.** A genus of 11 described species (Fig. 9), occurring in the Afrotropical, Nearctic, Oriental and Palaearctic Regions (Roháček *et al*. 2001: 53). Two species were recorded from the Afrotropics: *C. hackarsi* (Vanschuytbroeck, 1948), described from Democratic Republic of Congo; and *C. pedipicta* Richards, 1959, from Ethiopia. Species of the genus are largely coprophagous, but some species are terricolous (micro-cavernicolous, developing in burrows on droppings of small mammals), others are associated with dung of larger mammals. The puparium was described for extralimital species by Goddard (1938) and Skidmore (1993). For identification of the two Afrotropical species refer to Norrbom & Kim (1985*a*).

***Dudaia* Hedicke** (Copromyzinae)**.** An endemic genus of 20 described species (Fig. 2), distributed in Central, East, Southern and West Africa and the Indian Ocean Islands (Papp & Norrbom 2015). Additional undescribed species should be expected from the region. The biology of the genus is poorly known, but they are not predominantly coprophagous (few specimens have been collected on dung) and the immature stages remain unknown. *Dudaia* specimens are far less numerous in collections than those which are coprophagous and readily collectible from elephant dung and the dung of other large-bodied hoofed animals. An identification key to species was provided by Papp & Norrbom (2015).

***Elachisoma* Rondani** (Limosininae)**.** A genus of eight described species occurring in the Afrotropical, Nearctic, Oriental and Palaearctic Regions. Three species are recorded from the Afrotropics: *E. afrotropicum* L. Papp, 1983, recorded from Nigeria and South Africa; *E. aterrimum* (Haliday, 1833), from Saint Helena Is.; and *E. simillimum* L. Papp, 2017, from South Africa (Papp 1983, 2017). An additional record of the widely distributed species *E. aterrimum* from Democratic Republic of Congo is doubtful. Several additional undescribed species are expected to occur in the region. *Elachisoma* species are polysaprophagous and although mainly coprophagous, do not appear to develop on dung of specific mammal species. The puparium of *E. aterrimum* was described by Okely (1974). Papp (1983) treated the Old World species and provided an identification key that includes two of the three described Afrotropical species.

[***Eulimosina* Roháček** (Limosininae)**.** A genus of four described species occurring in the Oriental and Palaearctic Regions. Although the genus is not recorded from the Afrotropical Region, it is included in the above identification key, as its occurrence in the region seems likely. Adults are mainly associated with decayed vegetation in grassland habitats, but can also be attracted to dung (Roháček 1983). The immature stages remain unknown. An identification key to three extralimital species was provided by Papp (2008*b*), but an additional species was subsequently described by Su *et al*. (2013) from China.]

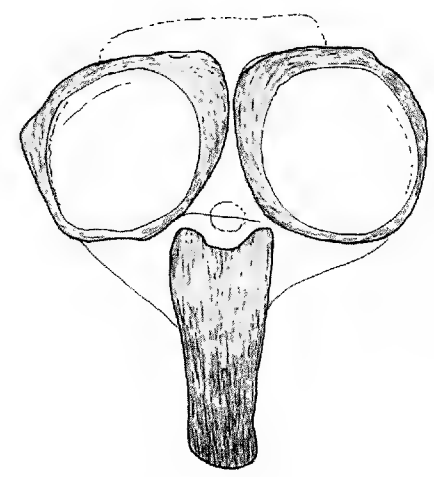
[***Eximilimosina* L. Papp** (Limosininae)**.** A genus of five or six (Hayashi 2011) described species occurring in the Oriental and eastern Palaearctic Regions. Although the genus is not recorded from the Afrotropical Region, it is included in the above identification key as its occurrence in the region seems likely. The immature stages and biology remain unknown, but at least some species are probably associated with humid forests. An identification key to four extralimital species was provided by Papp (2008*b*), but an additional species has subsequently described by Hayashi (2011).]

***Giraffimyiella* L. Papp** (Limosininae)**.** An endemic monotypic genus, with the single described species, *G. giraffa* (Richards, 1938) (Figs 3, 19), recorded from Burundi, Cameroon, Democratic Republic of Congo, Ethiopia, Kenya and Tanzania. Originally described as *Leptocera* (*Poecilosomella*) *giraffa* by Richards (1938), it was formerly included in the genus *Poecilosomella* for

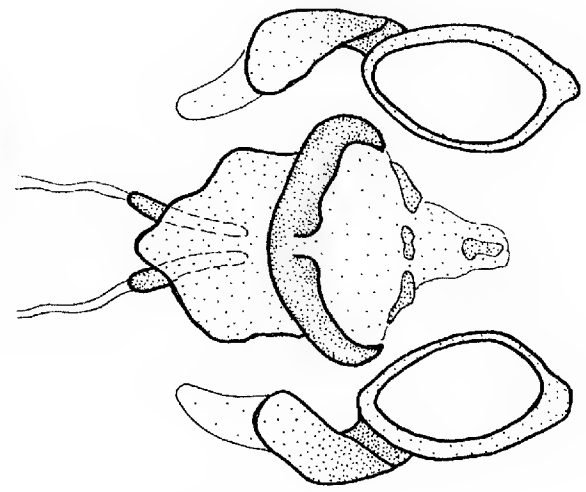
a considerable time. It is a patterned-winged species, having vein R_{2+3} slightly bent up to the costal vein (C) and very peculiar male terminalia (Figs 108, 122) (see also Papp 2008*b*: figs 88–92), that are markedly different to those of *Poecilosomella* species. The biology and immature stages remain unknown.

***Gobersa* de Coninck** (Limosininae)**.** An endemic monotypic genus, with the single subapterous species, *G. leleupi* de Coninck, 1983, confined to the Uluguru Mountains (Eastern Arc Mountains) of Tanzania and only known from the type material (de Connick 1983). The relationship of the genus to other apterous genera remain unclear, although the structure of the male terminalia (de Coninck 1983: figs 2A, 2B) indicates some affinity to *Paralimosina*. It differs, however, by the shape of the antennal postpedicel, with a distinctly projecting apex, the absence of the M-shaped mark on the frons and the male surstylus without distinct setae or spines. The type specimens were captured in humus under shrubs at 1,700 m (de Coninck 1983), but the immature stages remain unknown.

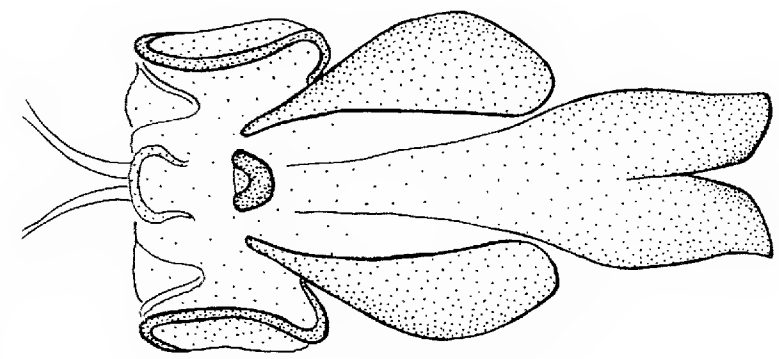
[***Gonioneura* Rondani** (Limosininae)**.** A genus of four described species occurring in the Nearctic, Neotropical,



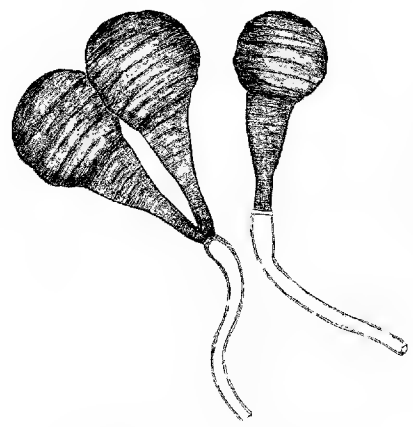
131 *Opacifrons* ♀



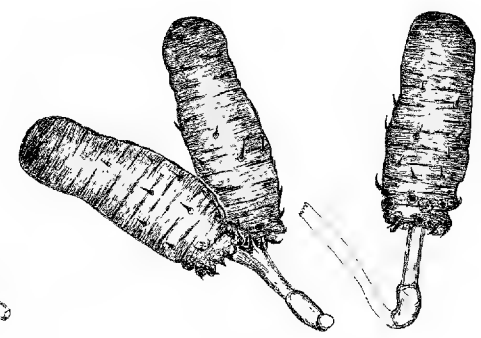
132 *Pullimosina* ♀



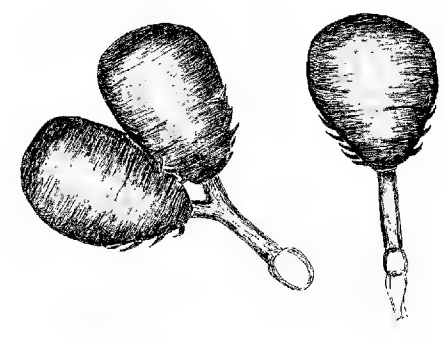
133 *Eulimosina* ♀



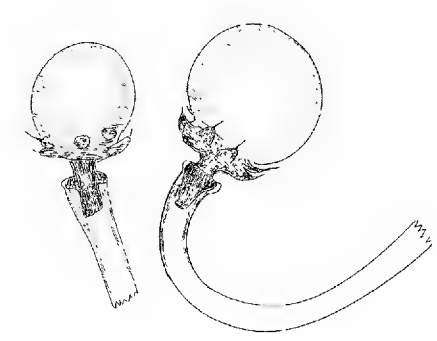
134 *Opacifrons* ♀



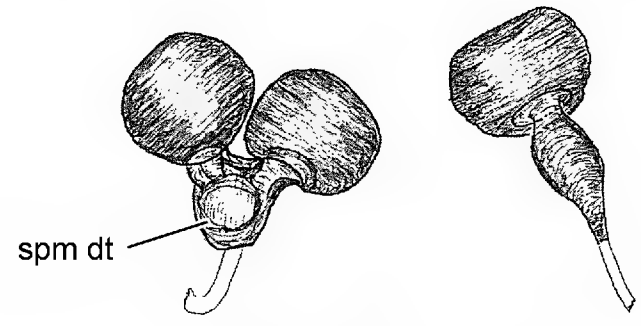
135 *Leptocera* ♀



136 *Leptocera* ♀



137 *Dudaia* ♀



138 *Chelilimosina* ♀

Figs 99.131–138. Female spectacles-shaped sclerites and spermathecae of Sphaeroceridae: (131) female spectacles-shaped sclerite of *Opacifrons subserrata* L. Papp, ventral view; (132) same, *Pullimosina moesta* (Villeneuve) (non-Afrotropical); (133) same, *Eulimosina ochripes* (Meigen) (non-Afrotropical); (134) spermathecae of *O. subserrata*, dorsal view; (135) same, *Leptocera kovacsi* Duda; (136) same, *L. marginata* (Adams); (137) same, *Dudaia communis* L. Papp & Norrbom; (138) same, *Chelilimosina baloghi* L. Papp. Figs 131, 134 (Papp 2012*a*, figs 52, 54), Fig. 132 (Roháček 1985, fig. 756), Fig. 133 (Roháček 1983, fig. 434), Figs 135, 136 (Papp 2012*b*, figs 41, 45), Fig. 137 (Papp & Norrbom 2015, fig. 12 © Magnolia Press), Fig. 138 (Papp 2014*a*, fig. 53 © Magnolia Press).

Abbreviation: spm dt – sperm duct.

Oceanian and Palaearctic Regions. Although the genus is not recorded from the Afrotropical Region, it is included in the above identification key as its occurrence in the region seems likely, particularly as regards the widespread *G. spinipennis* (Haliday, 1836). *Gonioneura* species are polysaprophagous, with larvae developing in decaying vegetation and dung where also adults occur (Marshall 1982; Roháček 1983). The puparium of the above extralimital species was described by Okely (1974). An identification key to three extralimital species was provided by Marshall (1982), but a fourth species was subsequently described by Marshall & Sun (1995) from China.]

***Gonitella* L. Papp** (Limosininae)**.** An endemic genus of three described species: *G. flavipes* L. Papp, 2008 and *G. structuralis* L. Papp, 2017, both described from Democratic Republic of Congo; and *G. inornata* L. Papp, 2017, described from South Africa (Papp 2017). The genus is mainly characterised by features of the male terminalia (Fig. 85): the surstylus is highly intricate, with three long ventrally directed lobes, the postgonite is extremely large (as long as the height of the epandrium) and the distiphallus has a ventrally directed process basally. Judging from the heavily sclerotised body and the fact that *G. flavipes* was sampled using pitfall traps in rainforest, the genus is terricolous. The immature stages remain unknown. No identification key to species is currently available, but the above species can be recognised by reference to Papp (2017).

***Gymnometopina* Hedicke** (Copromyzinae)**.** An endemic genus of 13 described species (Fig. 1), distributed in Central, East, Southern and West Africa and the Indian Ocean Islands, with most species restricted to tropical Africa. Two species, *G. clunicrus* (Duda, 1923) and *G. garambaensis* (Vanschuytbroeck, 1959), are widespread in the continental Afrotropics. Representatives of this genus invariably occur on dung, but the immature stages have not been described. Norrbom & Kim (1987) revised the genus and provided an identification key.

***Ischiolepta* Lioy** (Sphaerocerinae)**.** A genus of 32 described species, occurring in all zoogeographical regions, except Antarctica, with two virtually cosmopolitan species. Seven species are recorded from the Afrotropics, distributed in Central, East, Southern and West Africa and the Southern Arabian Peninsula, most restricted to the tropical belt (Roháček *et al*. 2001: 88). One coprophagous species, *I. scabricula* (Haliday, 1936), is probably of Afrotropical origin, but has been introduced through animal husbandry to the Nearctic, Neotropical, Oriental and Palaearctic Regions. The genus is primarily coprophagous to polysaprophagous, but some species are terricolous. The immature stages (egg and puparium) of extralimital species were described by Hinton (1981: 746), Okely (1974) and Skidmore (1993). Han & Kim (1990) revised all Afrotropical species and provided an identification key.

***Kabaria* Richards** (Limosininae)**.** An endemic monotypic genus, with the single brachypterous species, *K. spinisterna* Richards, 1966, described from the Kivu District, Democratic Republic of Congo. The species is characterised by the absence of postocellar setae, the wing is greatly reduced, but with a distinct rudiment, somewhat racket-shaped, without veins posterior to vein R_{4+5} and the halteres are normal, only slightly reduced in size. The abdomen lacks long setae, although male abdominal sternite 5 possesses robust setae and the male terminalia has the surstyli markedly asymmetrical (Richards 1966, figs 12, 13). Most type specimens were sampled in montane forest litter at elevations of 2,000–2,780 m (Richards 1966). The immature stages remain unknown.

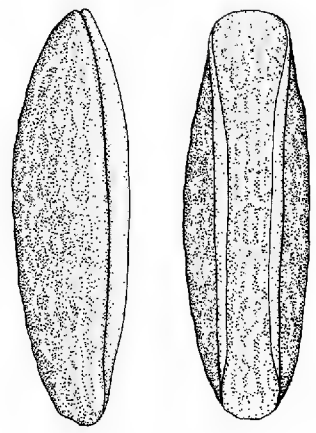
***Leptocera* Olivier** (Limosininae)**.** A large genus of more than 70 described species (Fig. 5), occurring in all zoogeographical regions, except Antarctica (Buck & Marshall 2009). Twelve species are recorded from the Afrotropics, distributed in Central, East, Southern and West Africa, the Atlantic and Indian Ocean Islands and the Southern Arabian Peninsula (Papp 2012*b*). Most species are known from South Africa, or are more widespread, with only a few species apparently restricted to equatorial Africa (Papp 2012*b*). *Leptocera caenosa* (Fig. 5), a virtually cosmopolitan species, due to its synanthropy, is known from South Africa and from Atlantic Gough I. (Jones *et al*. 2003) and *L. nigra* Olivier, 1813 (type species of the genus), is widespread in several zoogeographical regions and is distributed throughout the Afrotropics, including Saint Helena I. Most species are probably phytosaprophagous, but some are polysaprophagous. The puparia of extralimital species were described by Okely (1974), Richards (1930) and Skidmore (1993). Papp (2012*b*) treated the Afrotropical species and provided an identification key.

***Limosinella* Richards** (Limosininae)**.** An endemic monotypic genus, with the single described species, *L. munda* (Collin, 1912), first described from Seychelles as *Leptocera* (*Scotophilella*) *munda* and later recorded from South Africa, as *Limosinella polita* Richards, 1968 (synonymised by Roháček *et al*. 2001: 159). The species is probably terricolous and has been sampled in forest humus at elevations of 1,600–1,800 m in September and October (Richards 1968*c*). The immature stages remain unknown.

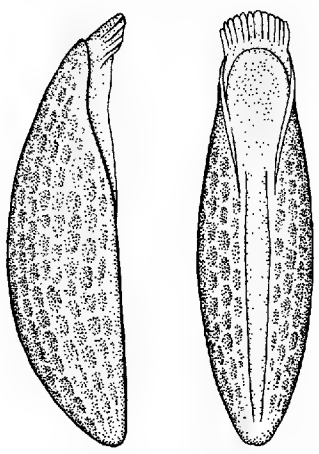
***Lobeliomyia* Richards** (Limosininae)**.** An endemic monotypic genus, with the single apterous species, *L. scotti* Richards, 1951, described from Mt Chillalo, Ethiopia. This species has the scutellum very short transverse and the abdomen markedly dilated (virtually circular in dorsal view) (Richards 1951*a*: 839, fig. 8). The unique female holotype was sampled from the decayed stem of *Lobelia* (Campanulaceae) in a high elevation (3,660–3,960 m) moorland habitat (Richards 1951*a*: 843). The immature stages remain unknown.

***Lotobia* Lioy** (Sphaerocerinae)**.** A genus of *ca* 30 described species (Fig. 10), occurring in the Afrotropical, Oriental and Palaearctic Regions. Twenty-four species occur in the Afrotropics, distributed in Central, East, Southern and West Africa, with most species known from Democratic Republic of Congo. *Lotobia* are coprophagous, with both larvae and adults occurring on dung of large mammals. The immature stages remain unknown. Kim & Han (1990) treated all described Afrotropical species and provided an identification key.

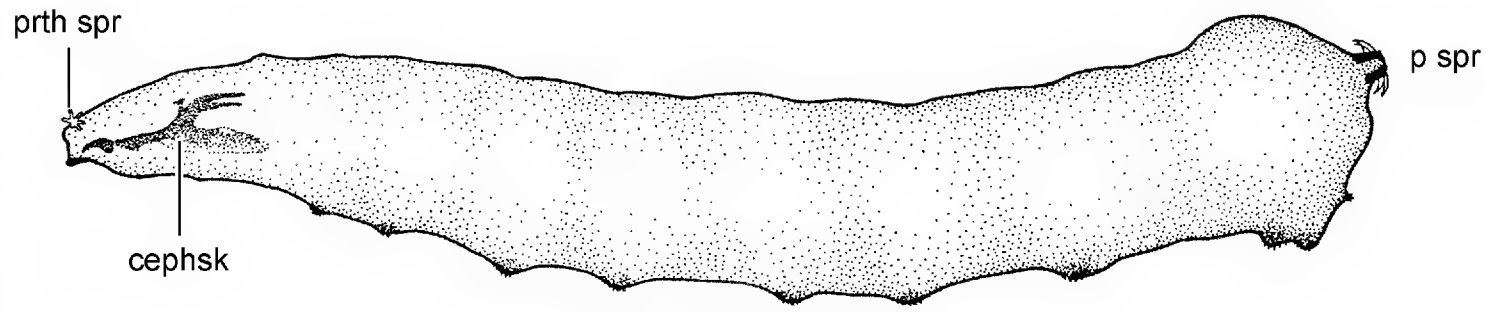
***Mesaptilotus* Richards** (Limosininae)**.** An endemic genus of 14 reduced-winged species, restricted to equatorial Africa, with most recorded from the Kivu Mountains, Democratic Republic of Congo (11 species), Mt Kilimanjaro, Tanzania (1), Rwanda (1) and the Ruwenzori Mountains, Uganda (1). Most species are apterous, but in some remnants of the wing are retained as minute scales. The abdomen is convex, but not strikingly wider than the thorax. Adults usually occur in humus, but also in moss beneath the plant *Senecio* (Asteraceae) and under stones, in damp montane forests at elevations of



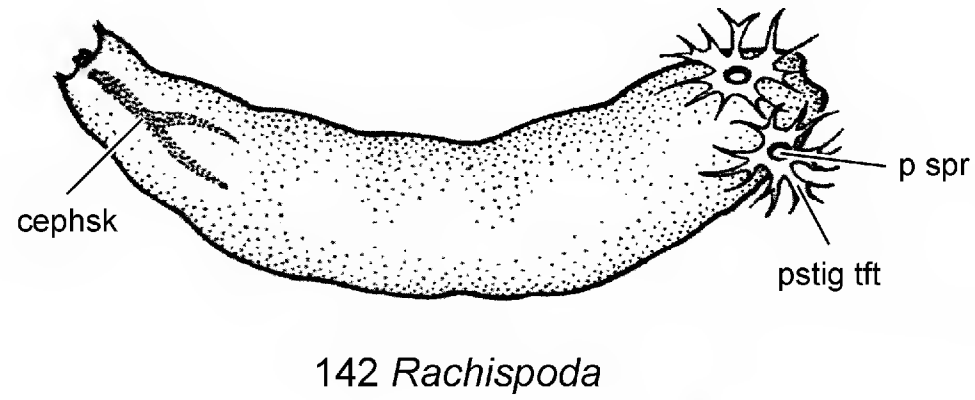
139 *Spelobia*



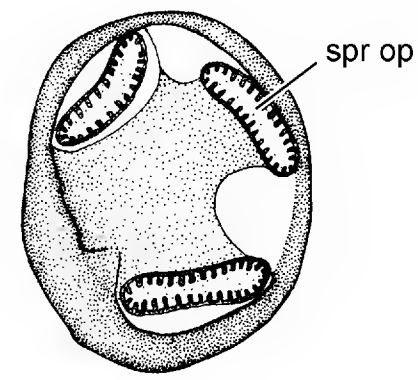
140 *Opalimosina* (*Opalimosina*)



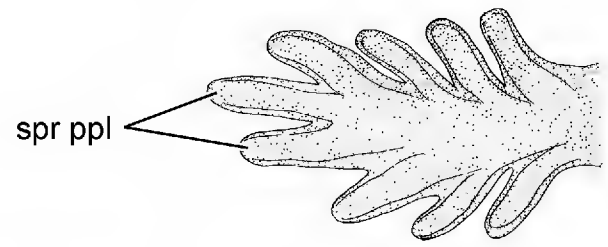
141 *Rachispoda*



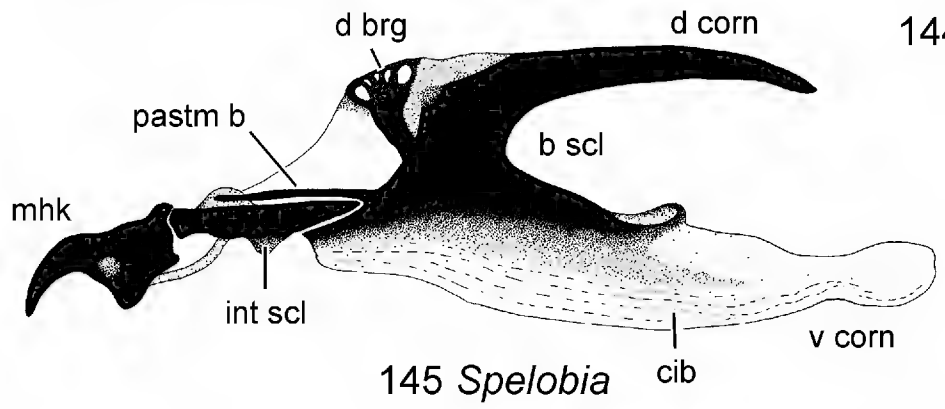
142 *Rachispoda*



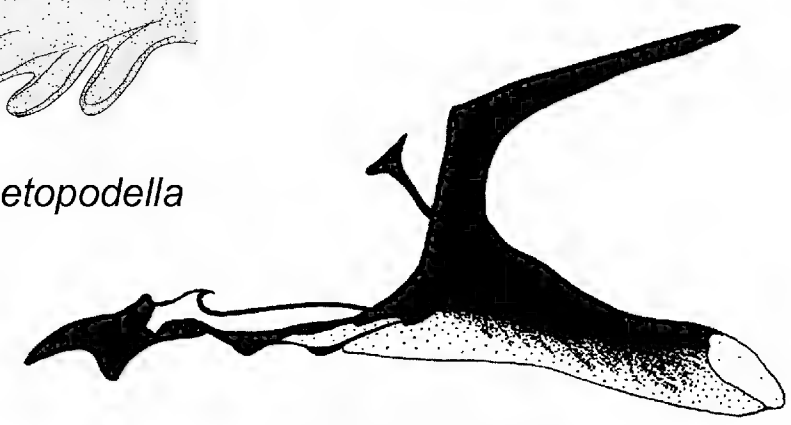
143 *Chaetopodella*



144 *Chaetopodella*

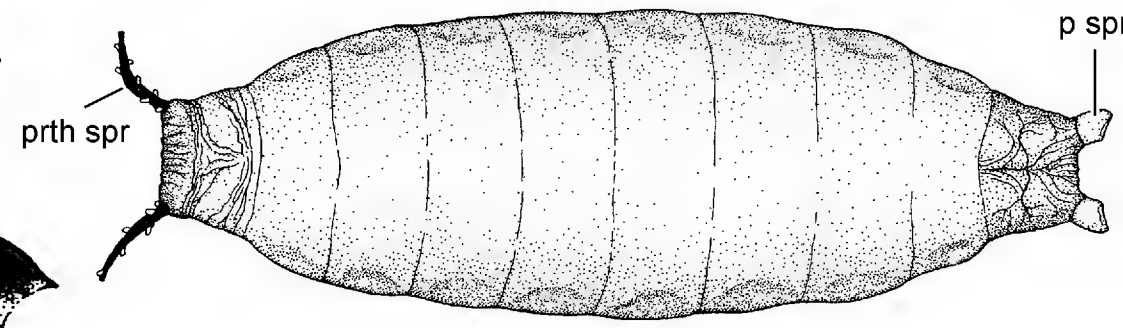


145 *Spelobia*



146 *Rachispoda*

147 *Rachispoda*



148 *Spelobia*

Figs 99.139–148. Immature stages of Sphaeroceridae: (139) egg of *Spelobia luteilabris* (Rondani), lateral view (left), dorsal view (right) (non-Afrotropical); (140) same, *Opalimosina* (*Opalimosina*) *simplex* (Richards) (non-Afrotropical); (141) habitus of third-instar larva of *Rachispoda fuscipennis* (Haliday), lateral view; (142) same, first-instar larva; (143) right posterior spiracle of third-instar larva of *Chaetopodella scutellaris* (Haliday), caudal view (non-Afrotropical); (144) same, prothoracic spiracle, lateral view; (145) cephaloskeleton of *S. palmata* (Richards), lateral view (non-Afrotropical); (146) same, second-instar larva of *R. fuscipennis*; (147) same, first-instar larva; (148) puparium of *S. parapusio* (Dahl), dorsal view. Figs 139, 140, 145, 148 (Roháček 1982, figs 2, 3, 5, 6, 7, 16), Figs 141, 142, 146, 147 (Mihara *et al*. 1983a, figs 3I, 3G, 3L, 3K), Figs 143, 144 (Schumann 1962, figs 34, 33, respectively).

Abbreviations: b scl – basal sclerite; cephsk – cephaloskeleton; cib – cibarium; d brg – dorsal bridge; d corn – dorsal cornu; int scl – intermediate sclerite; mhk – mouthhook; p spr – posterior spiracle; pastm b – parastomal bar; prth spr – prothoracic spiracle; pstig tft – peristigmatic tuft; spr op – spiracular opening; spr ppl – spiracular papillae; v corn – ventral cornu.

1,600–4,000 m (Richards 1963). The immature stages remain unknown. Richards (1963) treated all known species and included an identification key.

***Metaborborus* Vanschuytbroeck** (Copromyzinae)**.** A genus of 16 described species occurring in the Afrotropical and Oriental Regions. Thirteen species are known from the Afrotropics, distributed in Central, East and Southern Africa, indicating that the genus has its origin in the region (Norrbom & Kim 1985*b*). All species appear to be coprophagous and in some instances many thousands of specimens occur on fresh elephant and other large mammal dung. The immature stages remain unknown. Norrbom & Kim (1985*b*) described all Afrotropical species and provided an identification key.

***Minilimosina* Roháček** (Limosininae)**.** A genus of more than 80 described species, occurring in all zoogeographical regions, except Antarctica. The genus is divided into six subgenera (Marshall *et al.* 2011; Roháček *et al.* 2001), four of which occur in the Afrotropics. Three species are recorded from the Afrotropics, as outlined below. The subgenus *Minilimosina sensu stricto* is principally Holarctic, with the single Afrotropical species, *M.* (*M.*) *selecta* L. Papp, 2017, described from South Africa. There are, however, several undescribed species known from collections. *Minilimosina sensu stricto* species are generally saprophagous, developing in decaying vegetation and fungi, but also in rotting matter of animal origin. The subgenus *M.* (*Allolimosina* Roháček) is again largely Holarctic, but an undescribed species is known from the Afrotropics. The subgenus *M.* (*Amediella* L. Papp) is represented by *M.* (*Am.*) *endrodyi* L. Papp, 2008, the type species of the subgenus, which was recorded from Ghana and Republic of Congo, but there are probably several other undescribed species in the Afrotropical and Oriental Regions (Papp 2008*b*). The name *Amediella* is currently a homonym of *Amediella* Jaschhof (Jaschhof & Jaschhof 2003) and should be formally replaced in the future. Species of the subgenus have only been sampled as components of air plankton and in pitfall traps. The subgenus *M.* (*Svarciella* Roháček) is represented in most parts of the world, but is richest in the Oriental Region (Roháček & Marshall 1988). A single species, *M.* (*S.*) *rohaceki* L. Papp, 2017, was described from South Africa. The name of the last-named species is preoccupied by *Minilimosina* (*Minilimosina*) *rohaceki* (L. Papp, 1978) from Afghanistan and this homonymy should be formally resolved as part of a future revision of *Minilimosina*. The puparium of an extralimital species was described by Goddard (1938). No identification key to Afrotropical species is currently available, but for identification of the species listed above see Papp (2008*b*, 2017).

***Mislocatus* L. Papp** (Limosininae)**.** An endemic monotypic genus, with the single described species, *M. ealensis* (Vanschuytbroeck, 1951), recorded from Democratic Republic of Congo and South Africa (Papp 2014*a*). The species was formerly misplaced in the genus *Ceroptera*. The biology and immature stages remain unknown.

***Norrbomia* L. Papp** (Copromyzinae)**.** A genus of more than 30 described species (Fig. 6), occurring in all zoogeographical regions, except Antarctica. Twelve species are recorded from the Afrotropics, distributed in Central, East, Southern and West Africa, the Atlantic and Indian Ocean Islands and the Southern Arabian Peninsula, but additional undescribed species are known from the region. About half of these are widespread in the continental Afrotropics and others are restricted to the equatorial belt or to South Africa, while *N. stuckenbergi* (Hackman, 1967), appears to be endemic to Madagascar. All Afrotropical *Norrbomia* species are apparently coprophagous and mainly occur on dung of larger ungulates. The immature stages (egg and larva) of extralimital species were described by Schumann (1961, 1962) and Papp (1988, 2017) provided descriptions and an identification key to species.

***Nudopella* Roháček & Marshall** (Limosininae)**.** A genus of seven described species occurring in all zoogeographical regions, except the Neotropical Region and Antarctica. Four species are recorded from the Afrotropics, distributed in Southern Africa and the Southern Arabian Peninsula (Gatt 2008: 701). The genus was formerly regarded as a subgenus of *Trachyopella* Duda. Papp (2008*b*) reported *T.* (*Nudopella*) *operta* Roháček & Marshall, 1986 from the Afrotropical Region, but this record later proved to be a misidentification. More recently, Papp (2017) elevated the subgenus to generic rank and described three species: *N. erratica*, *N. marshalli* and *N. pseudoperta*, from the South Africa and noted at least one undescribed species close to *N. leucoptera* (Haliday, 1836) from the region. Afrotropical species are mainly associated with decaying plant material and the puparium of an extralimital species was described by Okely (1974). For the identification of Afrotropical species refer to Papp (2017), but no identification key was provided.

***Ocellipsis* Richards** (Limosininae)**.** An endemic genus of 13 described species (Fig. 25), all of which are recorded from the mountains of Kenya, mostly from Mt Elgon (9 species), the Aberdare Mountains (2) and the Marakwet escarpment (2). Species of the genus have the wings, halteres and ocelli absent; the scutellum is short and transverse and the abdomen broad to sub-circular (Fig. 25). Adult flies are terricolous, occurring on the forest floor in leaf litter, in moss and amongst grass and thistles in high-montane open (alpine grassland) and forested habitats, at elevations of 2,400–4,000 m (Richards 1957, 1963). The immature stages remain unknown. Richards (1965) reviewed the species and provided an identification key.

***Ocellusia* Séguy** (Limosininae)**.** A poorly described endemic genus of two apterous species: *O. achroma* Séguy, 1955 and *O. jugorum* Séguy, 1955, both confined to mountains of Madagascar. The two species are only known from the type material. According to Hackman (1967), the systematic position of this endemic Malagasy genus is not clear, but he believed it to be related to some of the wingless genera occurring in the continental Afrotropics. The two species are obviously terricolous, but the biology and immature stages are otherwise unknown. For identification of the two species refer to Séguy (1955).

***Oligochaetosella* L. Papp** (Limosininae)**.** An endemic monotypic genus, with the single described species, *O. inconspicua* L. Papp, 2014, described from Ghana. These are minute flies (body length: 1.1 mm), with the body not strongly sclerotised and not granulose and both the male and female terminalia peculiarly structured. The biology and immature stages remain unknown, as all known specimens were sampled as aerial plankton (Papp 2014*a*). For identification of the species refer to (Papp 2014*a*).

***Opacifrons* Duda** (Limosininae)**.** A genus of almost 40 described species, occurring in all zoogeographical regions,

except Antarctica. Six species are recorded from the Afrotropics, distributed in Central, East, Southern and West Africa and the Southern Arabian Peninsula (Papp 2012*a*), but additional undescribed species should be expected from the region (see also Gatt 2008: 700). The type species of the genus, *O. coxata* (Stenhammar, 1855), was formerly erroneously reported from the region. Most species occur on muddy shores of rivers, lakes and pools and in marshland habitats, the larvae probably developing in mud, but the immature stages remain unknown. For identification of Afrotropical species refer to Papp (2012*a*).

***Opalimosina* Roháček** (Limosininae)**.** A genus of four subgenera (Roháček *et al*. 2001: 179) and 15 described species, occurring in all zoogeographical regions, except Antarctica, with most (12 species) belonging to the nominate subgenus. The single species, *O.* (*Opalimosina*) *mirabilis* (Collin, 1902), has recently been recorded from South Africa (Papp 2017), but a few additional undescribed species of the nominate subgenus are known from collections. *Opalimosina* species are saprophagous, some more or less specialised on the dung of large ungulates, others develop in rotten plant material or decaying fungi (Roháček 1983). The immature stages of extralimital species (egg, larva and puparium) were treated by Okely (1974), Roháček (1982), Skidmore (1993) and Tenorio (1968).

***Oribatomyia* Richards** (Limosininae)**.** An endemic genus of two apterous species, *O. flavicans* Richards, 1960 and *O. flavelola* Richards, 1960, both described from the Kivu District, Democratic Republic of Congo (Richards 1960*a*). These are minute flies (body length: 1.5 mm) superficially resembling mites. The body is orange-brown and shiny, the ocelli are absent and the chaetotaxy of the frons is greatly reduced, with only the ocellar setae and the outer and inner vertical setae present. Adults occur in humus in bamboo montane forests at elevations of 2,000–2,850 m (Richards 1960*a*). The immature stages remain unknown. For identification of the two species refer to Richards (1960*a*).

***Paracuminiseta* L. Papp** (Limosininae)**.** An endemic monotypic genus, with the single described species, *P. tetraspinosa* L. Papp, 2008, described from Ghana and Guinea. The species was formerly thought to be close to the genus *Acuminiseta*, but based on the structure of the antenna, it appears to be closer to *Anommonia*. The male terminalia have simple preabdominal sternites and the intricate trilobed surstylus does not indicate a close relationship to *Acuminiseta*. According to Papp (2008*b*), there are two additional undescribed species known from collections. The biology and immature stages remain unknown, but the type specimens were collected at light.

***Paralimosina* L. Papp** (Limosininae)**.** An Old World genus of 46 described species, occurring in the Afrotropical, Oriental and Palaearctic Regions. Six species are recorded from the Afrotropics, distributed in East and Southern Africa (Papp 2013) and there are additional undescribed species known from collections. As apterous species are known from other zoogeographical regions, it cannot be ruled out that apterous species shall still be discovered in the Afrotropics. In the Afrotropics, adults are mostly found in indigenous forests (Papp 2013), where they are probably associated with rotting ground vegetation. The immature stages remain unknown. For identification of the six Afrotropical species refer to Papp (2013).

***Paramera* L. Papp** (Limosininae)**.** A genus of two described and two unnamed species, occurring in the Australasian and Oriental Regions (Papp 2008*b*). Undescribed species are known from Papua New Guinea and Thailand (Papp 2008*b*). The genus is not formally recorded from the Afrotropics, but an undescribed species is known from the region (L. Papp, unpubl.). The biology is poorly known, but adults of the extralimital species *P. robusta* L. Papp, 2008 were collected on domestic ox and elephant dung (Papp 2008*b*). The immature stages remain unknown.

***Paraminilimosina* L. Papp** (Limosininae)**.** A genus of three described species occurring in the Afrotropical and Oriental Regions. One described species is recorded from the Afrotropics, *P. similis* L. Papp, 2017, from Nigeria and Tanzania. The species appears to be elephant dung specialists (Papp 2008*b*, 2017). The immature stages remain unknown. No identification key is currently available, but for identification of *P. similis* refer to Papp (2017).

***Parapoecilosomella* L. Papp** (Limosininae)**.** An endemic genus of two described species: *P. formosa* L. Papp, 2017, described from Democratic Republic of Congo; and *P. lusingana* (Vanschuytbroeck, 1959), recorded from Democratic Republic of Congo and Republic of Congo. The type species of the genus, *Limosina lusingana*, was included in the genus *Poecilosomella* for a considerable period (Papp 2008*b*). Although *Parapoecilosomella* species also have distinctive wing patterning (Fig. 47), they differ from *Poecilosomella* in some characters, including features of the terminalia (Figs 91, 100). The biology and immature stages remain unknown. For identification of the two species refer to Papp (2008*b*, 2017).

***Paraptilotus* Richards** (Limosininae)**.** An endemic genus of nine described species, eight from the mountains of Kenya (Mt Elgon and the Aberdare Mountains) and one species, *P. discontinuus* (Richards, 1954), from Mt Tola, Ethiopia. All species of the genus are apterous, without halteres and postocellar setae, the mid tibia has paired setae at ⅓ and ⅘ of its length and the male surstylus is composed of 3 lobes, which bear black tooth-like setae. Adults occur in various forms of detritus, including moss and grass with *Lobelia* and *Senetio* (Asteraceae) in high-montane *Hagenia* (Rosaceae), *Senetio*, or bamboo forests, at elevations of 2,900–4,165 m. The immature stages remain unknown. An identification key to species was provided by Richards (1965).

***Permixtolimosina* L. Papp** (Limosininae)**.** An endemic monotypic genus, with the single species, *P. sexsetosa* L. Papp, 2014, described from South Africa. The type material was sampled in a Malaise trap, deployed in broad-leaved deciduous woodland (Papp 2014*a*). The biology and immature stages of the species remains unknown. For species verification see Papp (2014*a*).

***Philocoprella* Richards** (Limosininae)**.** A genus of seven described species occurring in the Afrotropical and Palaearctic Regions (Hayashi 2013; Roháček *et al*. 2001: 190). Only one species is recorded from the Afrotropics, *P. africana* L. Papp, 2017, described from South Africa (Papp 2017), but additional undescribed species should be expected from the region (Papp 2008*d*). Species of the genus are associated with dung of large mammals and *P. africana* was sampled in abundance

on elephant dung. The biology and immature stages remain unknown. For species confirmation refer to Papp (2017).

***Phthitia* Enderlein** (Limosininae)**.** A genus of *ca* 50 described species, occurring in all zoogeographical regions, except Antarctica. Five species are recorded from the Afrotropics, distributed in Southern Africa, the Atlantic Ocean Islands and the Southern Arabian Peninsula (Gatt 2008: 700). Three subgenera are represented in the region: *P.* (*Phthitia* Enderlein), *P.* (*Kimosina* Roháček) and *P.* (*Rufolimosina* L. Papp), but not all known species have been assigned subgeneric rank. A micropterous species, *P.* (*Phthitia*) *sanctaehelenae* (Richards, 1951), occurs on Saint Helena Is., which was originally described in the genus *Aubertinia* (Richards 1951*a*), and later synonymised under *Phthitia* by Marshall & Smith (1992). The widespread Holarctic species, *P.* (*K.*) *plumosula* (Rondani, 1880) was recorded as a probable introduction on Gough I. (Jones *et al*. 2003). *Phthitia* species are mostly associated with decaying vegetation (Roháček 1983), but their immature stages remain unknown. For identification of Afrotropical species refer to Marshall & Smith (1992) and Papp (2017).

***Piliterga* L. Papp** (Limosininae)**.** A genus of two described species occurring in the Afrotropical and Oriental Regions. One species is recorded from the Afrotropics, *P. africana* L. Papp, 2017, from Nigeria and Tanzania. The genus has the abdominal tergites de-sclerotised with extremely long tergal setae, the male terminalia have a distinct recurved dorsal process of the distiphallus and the female cerci are short, with short, straight and thick setae. The Oriental type species, *P. thaii* L. Papp, 2008, is not uncommon on elephant and domestic ox dung and *P. africana* has been collected from elephant dung, manure and the dung of larger hoofed mammals. The immature stages remain unknown.

***Pismira* Richards** (Limosininae)**.** An endemic genus of four described species (Fig. 24), all recorded from the Kivu District, Democratic Republic of Congo, where they occur at high-elevations (1,900–2,750 m). They are apterous, ant-like flies, with an extremely long pair of subbasal scutellar setae (Fig. 24), abdominal tergite 1 + 2 is considerably narrowed (petiolate) and strongly sclerotised. Adults are terricolous, occurring in soil humus in montane bamboo and *Hagenia* forests. Richards (1960*a*) treated all four species and provided an identification key.

***Poecilosomella* Duda** (Limosininae)**.** A genus of more than 60 described species (Figs 4, 17), occurring in all zoogeographical regions, except Antarctica. Fifteen species have been recorded from the Afrotropics, distributed in Central, East, Southern and West Africa and the Atlantic and Indian Ocean Islands (Papp 1990, 2010), but there are likely to be numerous undescribed species in the region. Species of the genus are distinctive, with a variegated body and wings (Figs 4, 17). The originally Afrotropical species *P. angulata* was introduced by human activity into South America and has spread northwards to the southern United States and was also introduced into the Palaearctic Canary Is. and Morocco. By contrast, the originally Oriental species *P. punctipennis* (Wiedemann, 1830) has spread to the Pacific basin, northwards to Hawaii and westwards into Afrotropical Zanzibar. Adults can be swept from vegetation in various open and forested habitats and may be attracted to dung (specimens repeatedly captured in dung traps). The immature stages remain unknown. Papp (2010) provided an identification key to Afrotropical species.

***Preepiphallus* L. Papp** (Limosininae)**.** An endemic genus of two described species: *P. endrodyi* L. Papp, 2014, from Burundi and Ghana; and *P. nitidifacies* L. Papp, 2014, from Malawi and South Africa. These are small species (body length: 1.5–2.2 mm), with the body not granulose, shiny or subshiny (*i.e.*, not microtomentose). The genus is principally characterised by the male terminalia, with the hypandrium without a ventral process and the basiphallus with a very long pre-epiphallus, but the epiphallus also long (Fig. 117). It does not fit either *Aptilotus*, or the Oriental genus *Trilobitella* L. Papp, with the right pregenital sclerites large, the surstylus undivided and rather compact and the ventral and apical parts with a peculiar structure composed of minute tubules. The male cerci do not meet sagittally, the postgonite is robust and the female spermathecae are long and cylindrical, thus much different from those of *Aptilotus* and *Paralimosina*. The biology remains largely unknown, but some specimens of *P. nitidifacies* were reared from hyrax (Procaviidae) droppings (Papp 2014*a*). The immature stages remain unknown. For identification of the two species refer to (Papp 2014*a*).

***Pseudaspinilimosina* L. Papp** (Limosininae)**.** An endemic monotypic genus, with the single species, *P. tanzan* L. Papp, 2008, described from Tanzania. This is one of the genera with the abdominal tergites de-sclerotised, with extremely long tergal setae (Fig. 77). The male terminalia are distinctive, with a very long, strongly sclerotised distiphallus with a separate additional dorsal sclerite and sternite 5 with a black posteromedial plate. The species has only been netted from elephant dung (Papp 2008*b*) and the immature stages remain unknown.

***Pseudocollinella* Duda** (Limosininae)**.** A genus of more than 40 species, occurring in all zoogeographical regions, except Antarctica. Five species are recorded from the Afrotropics, distributed in Burundi, Democratic Republic of Congo, Ghana, Namibia, South Africa and Tanzania, all in the subgenus *P.* (*Setiopacifrons* L. Papp). There are no Afrotropical examples of the nominate subgenus or of the remaining subgenus *P.* (*Spinotarsella* Richards), although *P.* (*Sp.*) *humida* (Haliday, 1836) has been repeatedly erroneously reported from the region. Species of subgenus *P.* (*Setiopacifrons*) are known to inhabit riverine and swampy habitats or on shores of creeks (Papp 2016). The immature stages remain unknown. An identification key to the five Afrotropical species was provided by Papp (2016).

***Pullimosina* Roháček** (Limosininae)**.** A genus of two subgenera (Roháček *et al*. 2001: 174) and *ca* 25 species, occurring in all zoogeographical regions, except Antarctica. Six species of the nominate subgenus are recorded from the Afrotropics, distributed in Central, East and Southern Africa, the Atlantic Ocean Islands and the Southern Arabian Peninsula (Gatt 2008: 700; Roháček *et al*. 2001: 174), including the virtually cosmopolitan *P. heteroneura*. The genus is, however, probably one of the most species-rich in the region, with dozens of additional undescribed species. *Pullimosina* species are generally phytosaprophagous (Roháček 1983) and occur in various decaying vegetation, including leaf litter in forests. The immature stages (eggs and puparia) of extralimital species were treated by Goddard (1938), Okely (1974) and Roháček (1982). The genus needs revision in the Afrotropics and no identification key to species is currently available.

[***Puncticorpus*** **Duda** (Limosininae)**.** A genus of three described species occurring in the Palaearctic Region. The genus is not recorded from the Afrotropics, but is likely to occur there, as there are records of one species from Morocco (Roháček *et al.* 2001: 223). All known species are terricolous and cavernicolous, occurring on the ground in forest litter or in subterraneous habitats and adults are often attracted to rotting fungi (Roháček & Marshall 1982). The immature stages remain unknown. An identification key to the three Palaearctic species was provided by Roháček & Marshall (1982).]

Rachispoda **Lioy** (Limosininae)**.** A genus of more than 160 species, occurring in all zoogeographical regions, except Antarctica (Roháček *et al.* 2001: 223). Fifteen species are recorded from the Afrotropics, distributed in Central, East, Southern and West Africa, the Atlantic and Indian Ocean Islands and the Southern Arabian Peninsula. There are many additional undescribed species from the region and the genus is in need of revision, following more extensive sampling. *Rachispoda* species are typically associated with muddy habitats, such as the shores of watercourses, lakes and oceans and various types of bogs, fens, saltmarshes, *etc*. The immature stages of *R. fuscipennis* (Haliday, 1833), a subcosmopolitan species also occurring in Afrotropics, were treated by Mihara *et al.* (1983*a*). The genus needs taxonomic revision in the Afrotropics and no identification key to species is currently available for the region.

Reunionia **L. Papp** (Limosininae)**.** An endemic monotypic genus, with the single apterous species, *R. unica* L. Papp, 1979 (Fig. 23), described from Réunion Is., known only from the type specimens. It is a terricolous species and was collected in detritus in indigenous forest (Papp 1979). The immature stages remain unknown.

Safaria **Richards** (Sphaerocerinae)**.** An endemic genus of eight described species (Figs 12, 13), distributed in Central, East and West Africa, in the tropical belt. One species, *S. brachyptera* Richards, 1966, is strongly brachypterous, having the wings only marginally longer than the thorax, with thickened veins, but with complete wing venation (Richards 1966, fig. 24). *Safaria* species appear to be terricolous and myrmecophilous, occurring in nests of doryline ants (Richards 1950, 1968*a*) and are clearly not coprophagous. The immature stages remain unknown. For identification refer to Richards (1950, 1968*a*).

Scutelliseta **Richards** (Limosininae)**.** An endemic genus of 18 species with reduced wings (apterous to brachypterous), occurring at low to middle elevations in South Africa and Swaziland. The genus is characterised by the apical scutellar setae, which are considerably longer than the basal scutellar setae, the prosternum is wide and the abdomen is without long outstanding setae. They are terricolous, occurring in humus in humid forests (Richards 1968*b*) and appear to be restricted to limited areas. The immature stages remain unknown. An identification key to known species (except for *S. mischogaster* Norrbom & Kim, 1985) (Norrbom & Kim 1985*c*) was provided by Richards (1968*b*).

Setositibiella **L. Papp** (Limosininae)**.** An endemic genus of two described species: *S. secunda* L. Papp, 2017, described from Burundi; and *S. terrestris* L. Papp, 2008, from Democratic Republic of Congo, but several additional undescribed species are known from the region. They are robust, fully winged flies, but the wings are narrow and they must be poor flyers, since the body is heavily sclerotised. Species of the genus are terricolous, but the immature stages remain unknown. For identification of the above species refer to Papp (2008*b*, 2017).

Spelobia **Spuler** (Limosininae)**.** A genus of *ca* 80 described species, occurring in all zoogeographical regions, except Antarctica (Roháček *et al.* 2001: 254). Two species are recorded from the Afrotropics: *S. foldvarii* L. Papp, 2017, described from Tanzania; and the introduced Palaearctic species *S. parapusio* (Dahl, 1909) on Gough I. (Jones *et al.* 2003), but at least two additional undescribed species are known from the region. *Spelobia* species are broadly polysaprophagous and occur in various decaying organic matter of plant and animal origin (Roháček 1983). The immature stages (eggs, larvae and puparia) have been described for *S. parapusio* and some extralimital species by Goddard (1938), Okely (1974), Roháček (1982) and Smith (1989: 206). For identification of the two species refer to Papp (2017) and Roháček (1983).

Sphaerocera **Latreille** (Sphaerocerinae)**.** A genus of seven described species, occurring in all zoogeographical regions, except Antarctica. Only one species is recorded from the Afrotropics, the virtually cosmopolitan *S. curvipes* (Fig. 8) from Ethiopia. This species is distributed around the world, because of animal husbandry and probably represents an introduction in the region. Although *Sphaerocera* species are polysaprophagous, most species appear to prefer the dung of large mammals. The immature stages of *S. curvipes* (eggs, larvae and puparia) were treated by Goddard (1938), Okely (1974), Skidmore (1993) and Smith (1989: 206). For identification see the redescription of *S. curvipes* by Kim (1968).

Spinilimosina **Roháček** (Limosininae)**.** A genus of six described species, occurring in all zoogeographical regions, except Antarctica. Two described species are recorded from the Afrotropics: *S. brevicostata* (Duda, 1918), from Democratic Republic of Congo, Ethiopia, Madagascar and South Africa; and *S. rufifrons* (Duda, 1925), from Democratic Republic of Congo and Ethiopia (Roháček *et al.* 2001: 267), but many additional undescribed species are known from collections. Adults occur on various decaying organic matter, including dung and the immature stages (egg and puparium) of *S. rufifrons* were treated by Tenorio (1968). For identification of the two species refer to Tenorio (1968) and Roháček (1983).

Subacuminiseta **L. Papp** (Limosininae)**.** An endemic monotypic genus, with the single described species, *S. minor* L. Papp, 2014, described from Ghana. This is a very small species (body length: 1.1–1.15 mm), with particularly sparse setae on the body and legs (Papp 2014*a*). The biology and immature stages remain unknown and the type specimens were captured as aerial plankton (Papp 2014*a*).

Telomerina **Roháček** (Limosininae)**.** A genus of 20 described species, occurring in all zoogeographical regions, except Antarctica. Only one species is recorded from the Afrotropics, the virtually cosmopolitan *T. flavipes* from South Africa (Papp 2017). The species is distributed around the world through animal husbandry and probably represents an introduction in the region. Species of this genus most closely resemble *Opalimosina*, but differ in having numerous additional setulae on the fronto-orbital plates and in front of the compound eye, the male terminalia (Fig. 83) have the epandrium ventromedially open (the subanal plate is not developed) and the subepandrial sclerite is entirely

absent. *Telomerina* species are mainly associated with dung (Roháček 1983), which is also true for *T. flavipes*. The puparium of *T. flavipes* was described by Skidmore (1993).

***Terrilimosina* Roháček** (Limosininae)**.** A genus of 16 described species occurring in the Afrotropical, Nearctic, Oriental and Palaearctic Regions. Only one species is recorded from the Afrotropics, *T. improvisa* L. Papp, 2017, described from Democratic Republic of Congo (Papp 2017). This species is a close relative of the Holarctic cavernicolous species *T. racovitzai* (Bezzi, 1911). *Terrilimosina* species are mostly terricolous or cavernicolous, with adults occurring in upper layers of forest litter or in various subterraneous habitats (burrows of mammals, caves, *etc.*). The puparium of an extralimital species was described by Skidmore (1993). Refer to Roháček (1983) for a diagnosis of the genus and Papp (2017) for species confirmation.

***Thoracochaeta* Duda** (Limosininae)**.** A genus of 35 described species (Fig. 15), occurring in all zoogeographical regions, except Antarctica (although recorded from sub-Antarctic Kerguelen Is.) (Hayashi 2005; Roháček *et al*. 2001: 274). The genus occurs mainly on marine shorelines and six species are recorded from the Afrotropics, distributed in Southern and West Africa, the Atlantic and Indian Ocean Islands and the Southern Arabian Peninsula. Four species are native to the region and two are virtually cosmopolitan, *i.e.*, *T. brachystoma* and *T. zosterae*, the latter probably recently introduced to Gough I. (Jones *et al*. 2003). At least one unnamed species was noted by Jones *et al*. (2003) from Gough I. and additional undescribed species are to be expected from the Indian and Atlantic Ocean seaboards. The four native Afrotropical species form a distinctive *T. securis* species-group, distinguished by the peculiarly bulging male sternite 5, the expanded spoon-shaped hypandrium and the reduced female tergite 6 and/or 7 (Marshall & Roháček 2000). All species are primarily associated with kelp and other marine algae on marine coasts, where their halophilous larvae develop. The immature stages of *T. zosterae* and some extralimital species (all stages) were treated by Egglishaw (1961), Skidmore (1993), Smith (1989: 206) and Tenorio (1968). Afrotropical species were revised by Marshall & Roháček (2000) and identification keys to Afrotropical species were provided by Kirk-Spriggs *et al*. (2001) (Namibia and South Africa) and Marshall & Roháček (2000) (the Afrotropical Region as a whole).

***Trachyopella* Duda** (Limosininae)**.** A genus of 29 described species, occurring in all zoogeographical regions, except Antarctica. Three species are recorded from the Afrotropics, all in the subgenus *Trachyopella sensu stricto*: *T.* (*T.*) *pannosa* Roháček & Marshall, 1986, described from Yemen; and two questionable species: *T.* (*T.*) *atomus* (Rondani, 1880) and *T.* (*T.*) *coprina* (Duda, 1918), both reported from Democratic Republic of Congo, plus additional undescribed species known from the region. No species in the subgenus *T.* (*Insulomyia* L. Papp) are recorded, but the subgenus is expected to occur in the region and is, therefore, included in the above identification key. The former subgenus *T.* (*Nudopella* Roháček & Marshall) was elevated to generic rank by Papp (2017) and so is not considered here. Marshall & Montagnes (1990) and Roháček *et al*. (2001: 280) synonymised all subgenera, except *T.* (*Nudopella*), under *Trachyopella*, but the subgeneric concept of *T.* (*Insulomyia*) (as delimited by Roháček & Marshall 1986: 34) is accepted here. *Trachyopella* are minute flies (body length: 0.7–1.2 mm), with a deep and high head, a broad frons, a large frontal lunule, small compound eyes and an extensive cephalic chaetotaxy, with distinct lateroclinate inner fronto-orbital setae (as in *Nudopella*, Fig. 27). *Trachyopella* species are associated with various rotting matter (particularly of plant origin) and the immature stages of extralimital species (eggs and puparia) were treated by Goddard (1938), Okely (1974) and Skidmore (1993). Species of *Trachyopella* are relatively well-documented for other regions of the world (Marshall & Montagnes 1990, for the Pacific region and Roháček & Marshall 1986, for the Holarctic Realm), but the Afrotropical species require revision and no identification key is currently available.

***Trichosphaerocera* L. Papp** (Sphaerocerinae)**.** An endemic monotypic genus, with the single described species, *T. africana* Papp, 1978 (Fig. 11), described from Lefinie Reservation, Republic of Congo. The type material comprises four males sampled in pitfall traps in elephant dung. No additional specimens have been collected and the biology and immature stages remain unknown. For species confirmation see Papp (1978).

***Trisetomyia* Richards** (Limosininae)**.** An endemic monotypic genus, with the single apterous species, *T. triseta* (Richards, 1954), described from Simien, Ethiopia, at high elevation, almost 4,000 m. All type specimens were collected from debris in dead and rotting stems of *Lobelia*. The species has not been collected subsequently and the immature stages remain unknown. For species confirmation refer to Richards (1954).

Undescribed genus (Limosininae)**.** A probable undescribed endemic genus is known from the region, comprising two described species: *Leptocera* (*Poecilosomella*) *multicolor* Richards, 1968, with its subspecies, known from Rwanda, South Africa and Zimbabwe; and *L.* (*P.*) *pictitarsis* Richards, 1938, from Democratic Republic of Congo, Kenya and South Africa. These species form a distinctive group of Afrotropical species (Papp 1990, 2008*b*) which probably represent a separate genus. The biology and immature stages remain unknown.

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EPHYDRIDAE 100

(Shore Flies)

Wayne N. Mathis, Tadeusz Zatwarnicki and Anthony G. Irwin

Fig. 100.1. *Dryxo ornata* (Macquart) (Tanzania) (photograph © S.A. Marshall).

Diagnosis

Minute- to medium-sized acalyptrate flies (body length: 0.6–11.0 mm), usually dull and dark coloured (Fig. 1), often clothed in whitish, greyish, or brownish micro-tomentum, but unusually diverse in body structure, vestiture and ornamentation; female usually larger than male; immature stages mostly aquatic or associated with aquatic habitats.

Head, including sub-cranial cavity, large (Figs 7–11, 14–95); 1–3, rarely up to 5 lateroclinate or reclinate/proclinate fronto-orbital setae; pseudopostocellar setae divergent or absent; antennal arista pectinate on dorsum only (Figs 9–11), or bare to pubescent (Figs 7, 8, 12); face flat to conspicuously protruding.

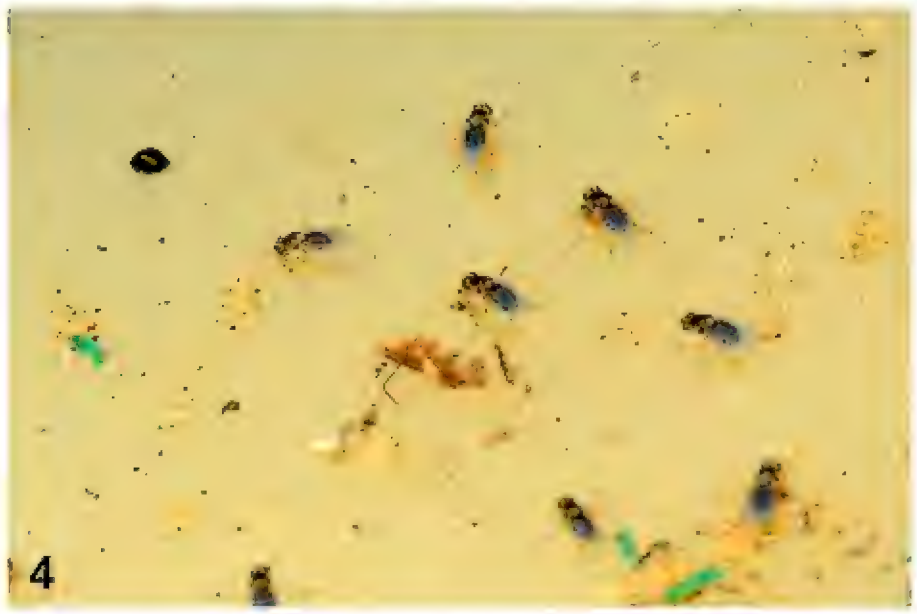
Thorax with scutum (Figs 96–102) usually bearing numerous acrostichal setulae, 1–5 dorsocentral setae, 2 or 3 supra-alar setae, 1 postalar seta; anepisternum setulose. Wing (Figs 105–113) usually well-developed; membrane hyaline (Figs 107, 108), but sometimes maculate (Figs 105, 106, 110–113); costal vein (*C*) with humeral and subcostal breaks (Fig. 105); subcostal vein (*Sc*) incomplete (Fig. 105); vein R_1 merging with costal vein (*C*) before middle of wing (Fig. 105); basal medial (*bm*) and discal medial (*dm*) cells confluent, basal medial crossvein (*bm–m*) and anterior cubital cell (*cua*) absent (Fig. 105). Legs (Figs 115–117) without preapical dorsal seta on fore and hind tibiae.

Abdomen of male commonly with 5 exposed tergites (Fig. 118); female with 6 or 7 exposed tergites (Fig. 120); abdominal

spiracles 1–5 located in tergites, spiracle 6 in pleural membrane near genital capsule; male terminalia (Figs 118, 119) symmetrical; female (Fig. 120) usually with 2 spermathecae, rudimentary, probably non-functional; ventral receptacle (Fig. 120) heavily sclerotised, functioning in place of spermathecae.

Egg (Fig. 121) white to greyish white (length: 0.30–1.30 mm; width: 0.14–0.49 mm), usually ellipsoidal ovoid, often with flattened surface, although contours generally symmetrical, except near ends; ends bluntly rounded to sub-bulbous; micropylar end sometimes drawn-out, forming elongate process or horn of varying length (some species of *Ochthera* Latreille), usually with small, narrowly campanulate "nipple"; chorion micro-reticulate to deeply rugose, sometimes with longitudinal ridges; ridges sometimes forked (as in *Discocerina obscurella* (Fallén, 1813) and *Hydrellia* Robineau-Desvoidy).

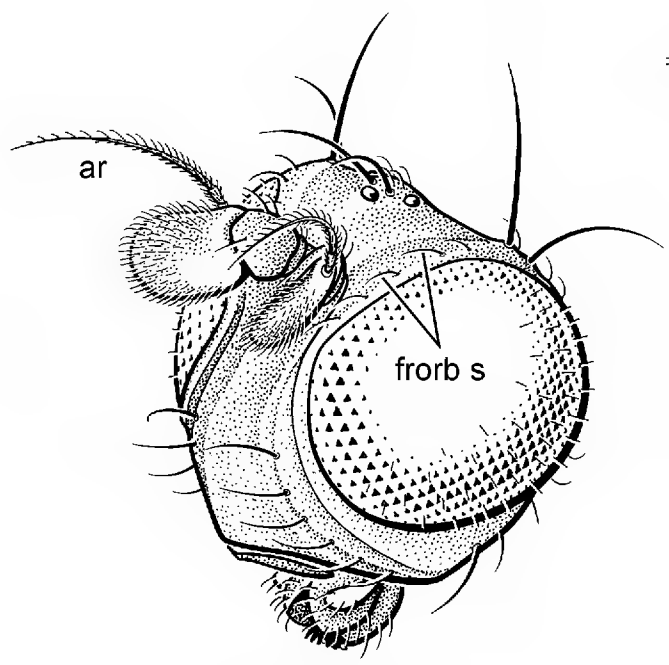
First-instar larva with metapneustic respiratory system, as small as 0.30 mm in length (*Scatophila* Becker); second- and third-instar larvae with amphipneustic respiratory system; third-instar larva (Figs 122, 123) reaching 18 mm (*Ochthera*); some earlier instars more spinulose, but most instars generally similar, except for size.



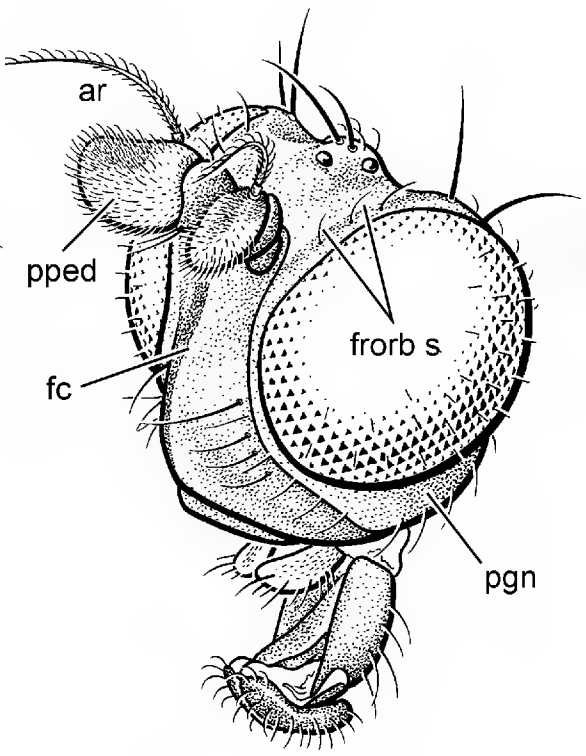
Figs 100.2–6. Photographs of living Afrotropical Ephydridae: (2) *Athyroglossa* (*Parathyroglossa*) *africana* (Wirth) (South Africa); (3) *Parydra* (*Parydra*) *bucculenta* Loew (Namibia); (4) *Brachydeutera* sp. (South Africa); (5) *Rhynchopsilopa* sp. (South Africa); (6) *Scatella* (*Neoscatella*) *stuckenbergi* Wirth (South Africa). Figs 2–6 (photographs © S.A. Marshall).

Puparium broadly similar to third-instar larva, but more compact, darker in colour (light yellow to greyish brown), hardened, integumental spinules more prominent than on larva and prothoracic respiratory processes fully extended, with distinctive features, such as dorsal cephalic cap; in species with more maggot-like larvae, puparium normally shorter and broader than larva, but in species with elongate larvae, such as those of *Ephydra* Fallén, with relatively little change of form; larval respiratory tube and spiracles extended fully at pupariation; in *Ephydra* anal proleg particularly large and curved forward at pupariation to grip substrate (usually an aquatic plant).

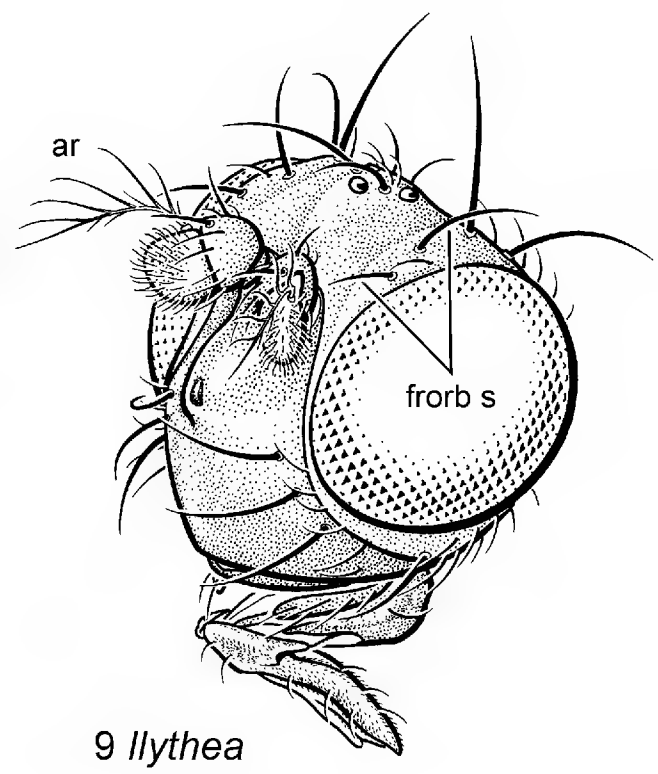
Although similar to some species of the families Chloropidae (see Chapter 96), Diastatidae (see Chapter 104) and Drosophilidae (see Chapter 106), Ephydridae are distinguished by the non-plumose antennal arista (pectinate on dorsal surface only), the costal wing breaks (a humeral and subcostal break), the confluent cells *bm* and *dm*, having only five abdominal tergites



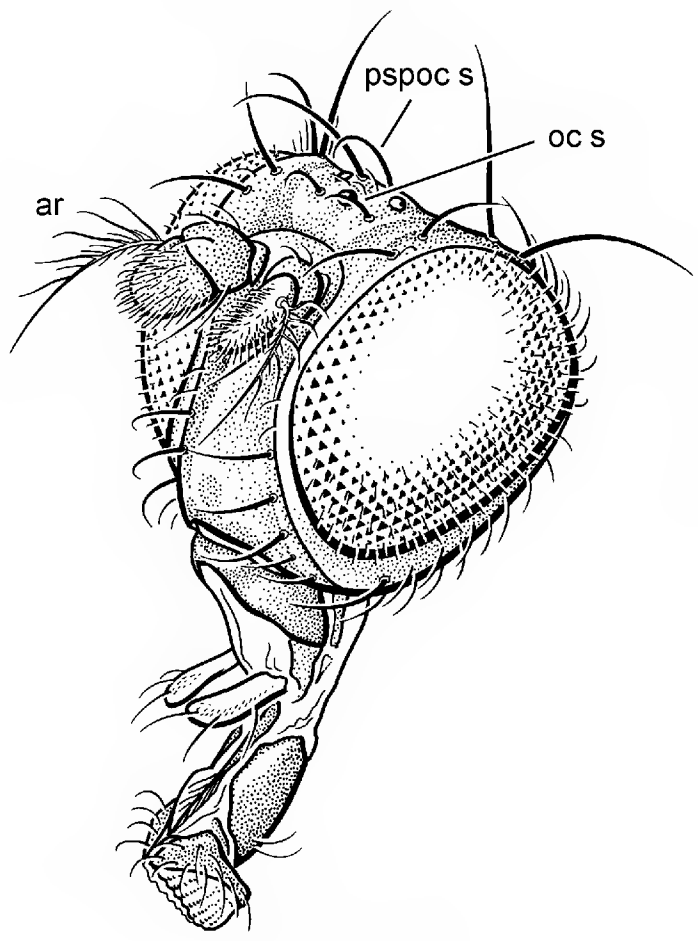
7 *Philygria*



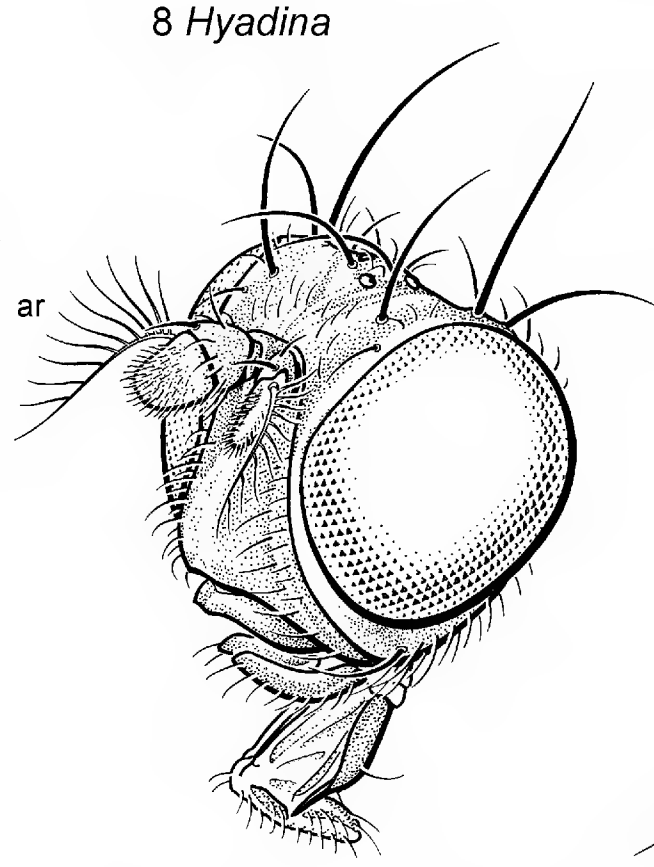
8 *Hyadina*



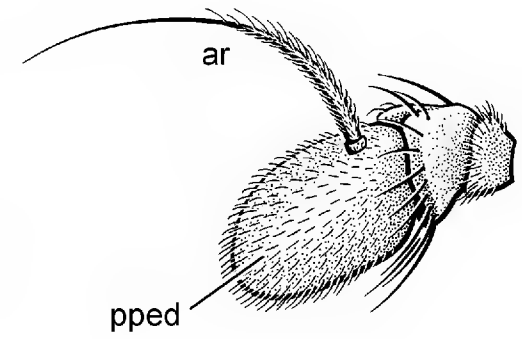
9 *Ilythea*



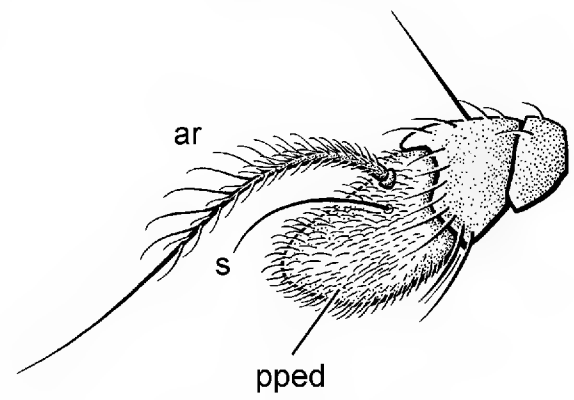
10 *Hydrellia*



11 *Notiphila* (*Agrolimna*)



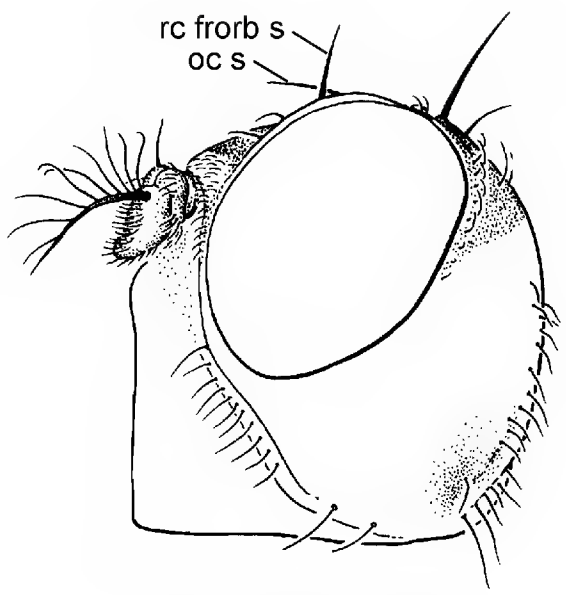
12 *Pelina*



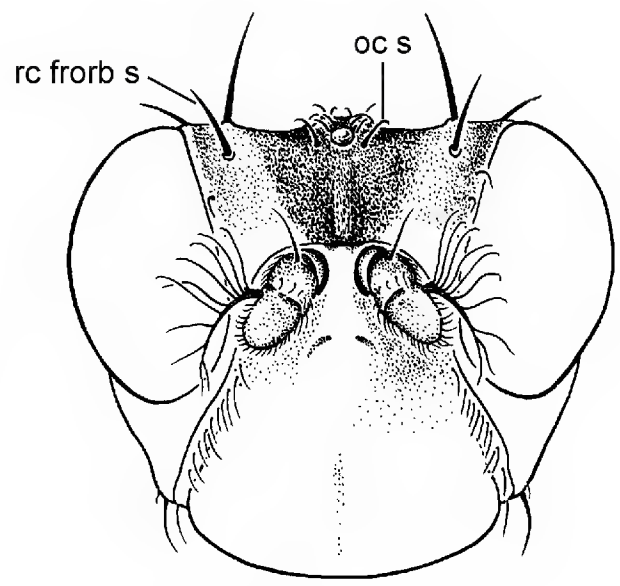
13 *Setacera*

Figs 100.7–13. Heads and antennae of Ephydridae (all non-Afrotropical): (7) head of *Philygria debilis* Loew, anterolateral view; (8) same, *Hyadina binotata* (Cresson); (9) same, *Ilythea spilota* (Curtis); (10) same, *Hydrellia griseola* (Fallén); (11) same, *Notiphila* (*Agrolimna*) *scalaris* Loew; (12) antenna of *Pelina truncatula* Loew, lateral view; (13) same, *Setacera pacifica* (Cresson). Figs 7–13 (Wirth *et al*. 1987, figs 36, 37, 28, 29, 31, 42, 43, respectively).

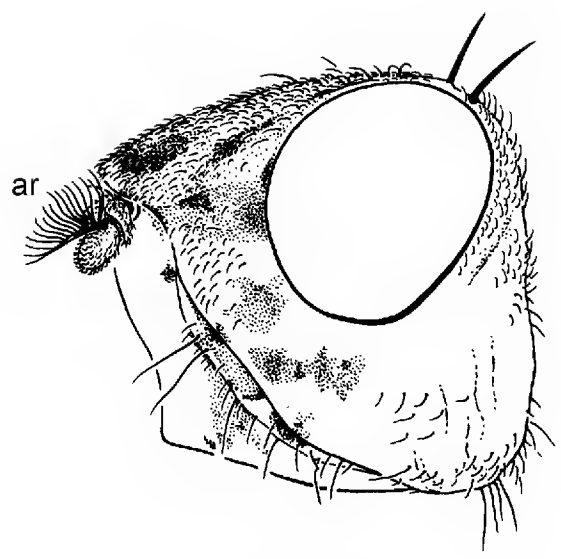
Abbreviations: ar – arista; fc – face; frorb s – fronto-orbital setae; oc s – ocellar seta; pgn – postgena; pped – postpedicel; pspoc s – pseudopostocellar seta; s – seta.



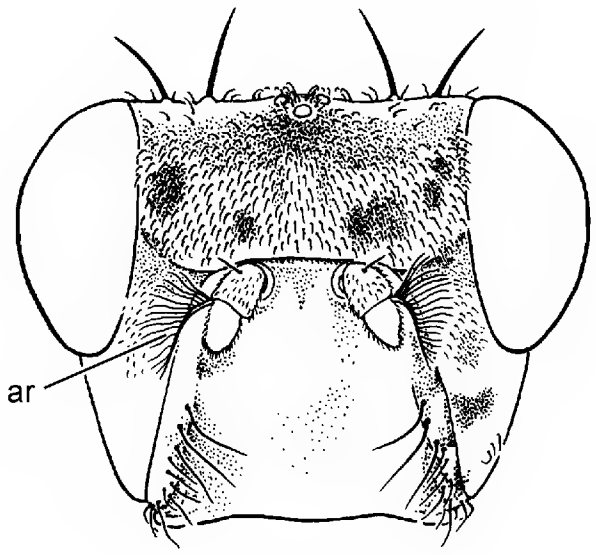
14 *Corythophora*



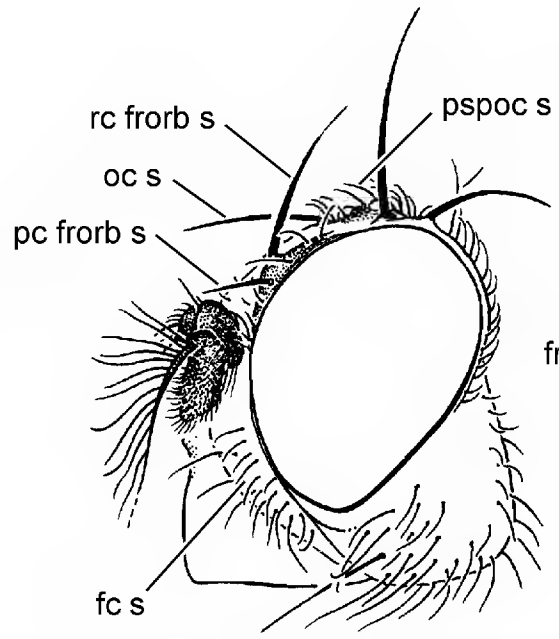
15 *Corythophora*



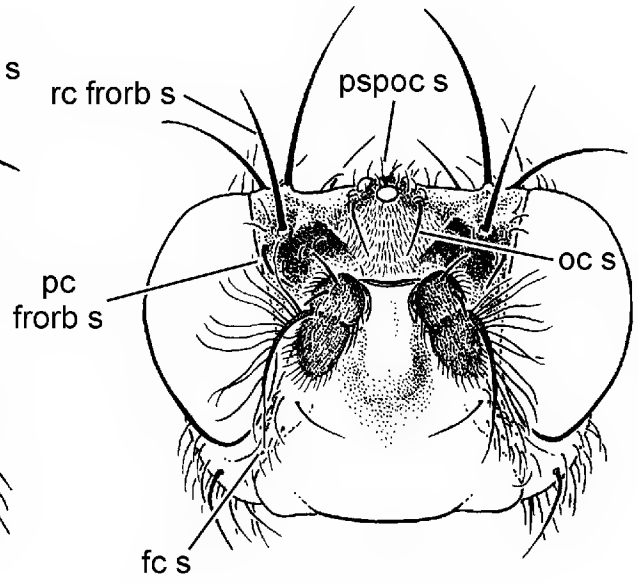
16 *Dryxo*



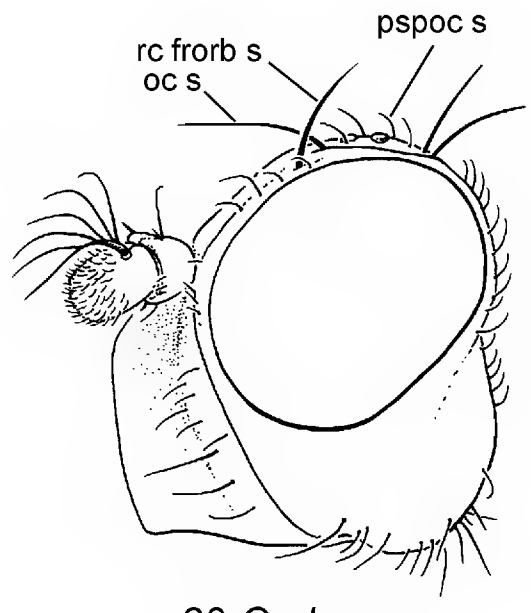
17 *Dryxo*



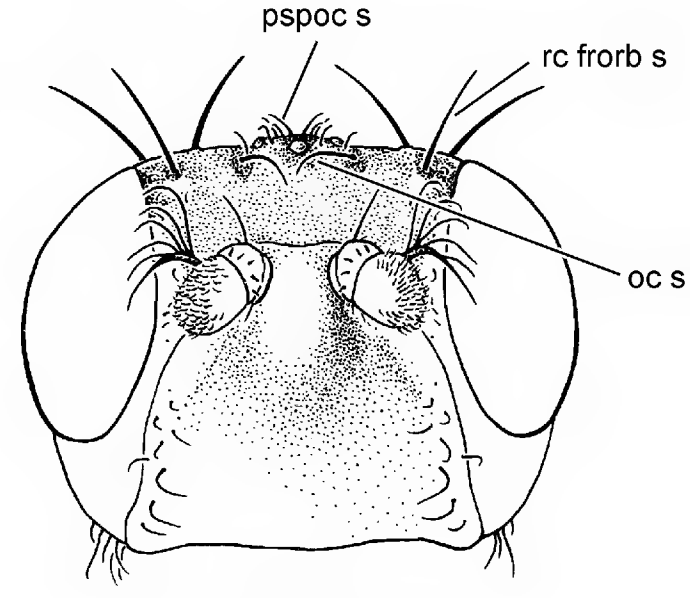
18 *Afrolimna*



19 *Afrolimna*



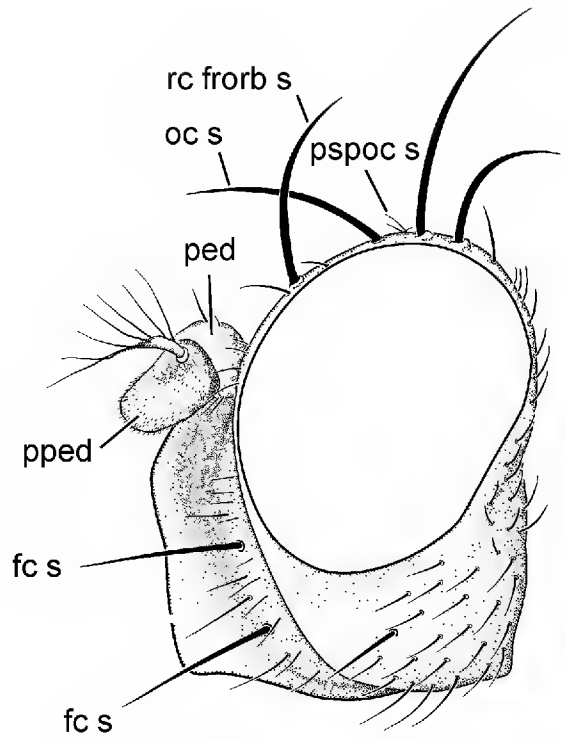
20 *Oedenops*



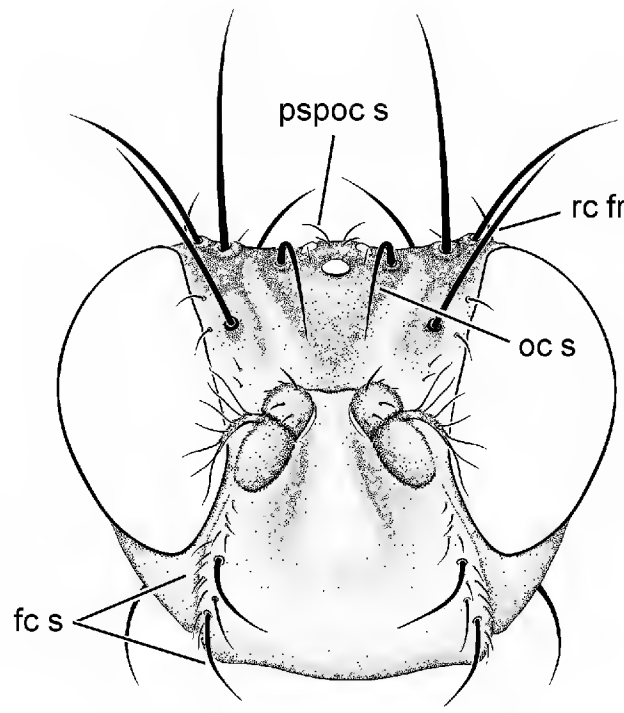
21 *Oedenops*

Figs 100.14–21. Heads of Ephydridae: (14) *Corythophora longipes* Loew, lateral view; (15) same, anterior view; (16) *Dryxo ornata* (Macquart), lateral view; (17) same, anterior view; (18) *Afrolimna carolinica* (Cogan), lateral view; (19) same, anterior view; (20) *Oedenops nudus* (Coquillett), lateral view (non-Afrotropical); (21) same, anterior view. Figs 14–21 (Mathis & Zatwarnicki 2002, figs 18, 17, 46, 45, 4, 3, 80, 79, respectively).

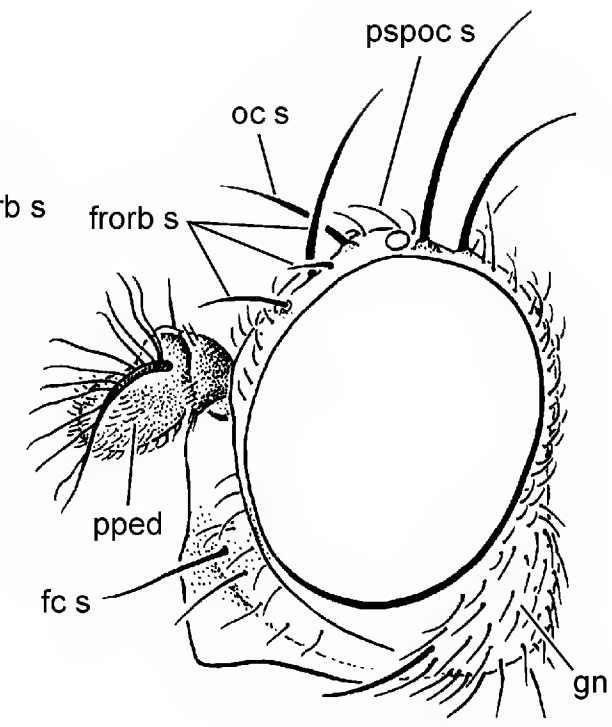
Abbreviations: ar – arista; fc s – facial setae; oc s – ocellar seta; pc frorb s – proclinate fronto-orbital seta; pspoc s – pseudopost-ocellar seta; rc frorb s – reclinate fronto-orbital seta.



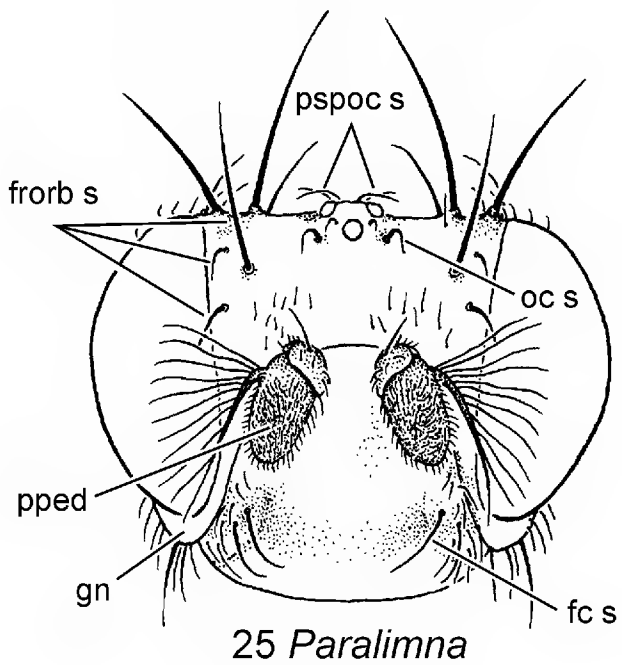
22 *Oedenopiforma*



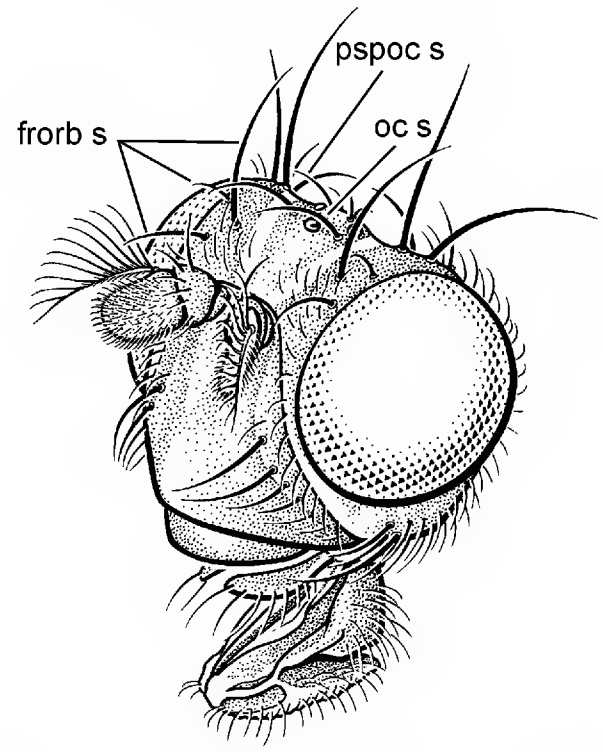
23 *Oedenopiforma*

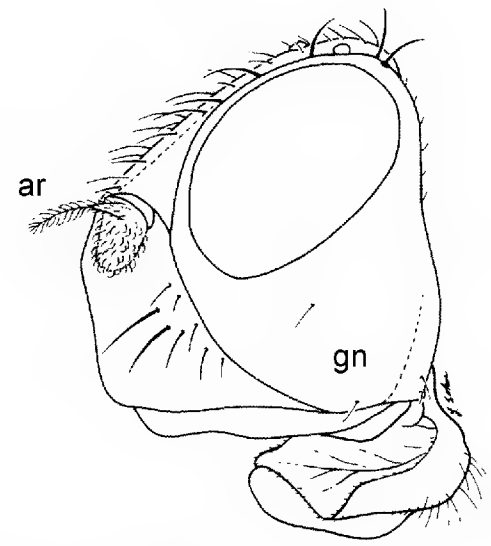


24 *Paralimna* (*Phaiosterna*)

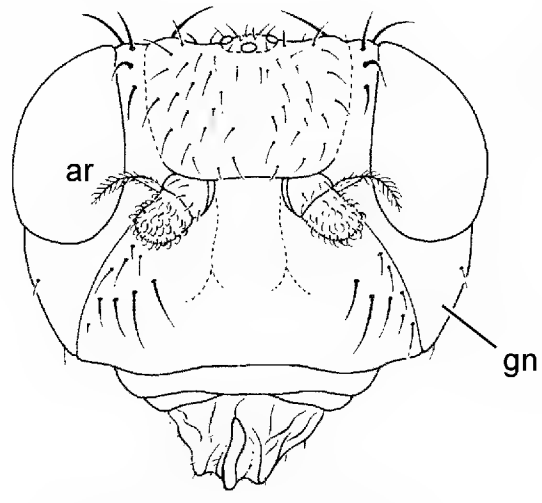


25 *Paralimna* (*Phaiosterna*)



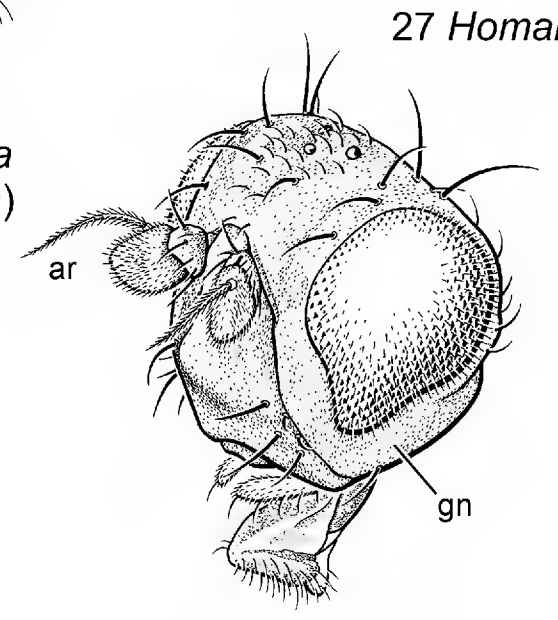


27 *Homalometopus*



28 *Homalometopus*

26 *Paralimna* (*Phaiosterna*)



29 *Glenanthe*

Figs 100.22–29. Heads of Ephydridae: (22) *Oedenopiforma vockerothi* Mathis & Zatwarnicki, lateral view; (23) same, anterior view; (24) *Paralimna* (*Phaiosterna*) *decipiens* Loew, lateral view (non-Afrotropical); (25) same, frontal view; (26) same, antero-lateral view; (27) *Homalometopus albiditinctus* Becker, lateral view; (28) same, anterior view; (29) *Glenanthe interior* Chillcott (non-Afrotropical), anterolateral view. Figs 22, 23 (Mathis & Zatwarnicki 2012*b*, figs 10, 9, respectively), Figs 24, 25 (Mathis & Zatwarnicki 2002, figs 117, 116, respectively), Figs 26, 29 (Wirth *et al*. 1987, figs 32, 25, respectively), Figs 27, 28 (Mathis 1984*b*, figs 5, 4, respectively).

Abbreviations: ar – arista; fc s – facial seta(e); frorb s – fronto-orbital setae; gn – gena; oc s – ocellar seta; ped – pedicel; pped – postpedicel; pspoc s – pseudopostocellar seta; rc frorb s – reclinate fronto-orbital seta.

in males and an internal female reproductive system that includes two rudimentary spermathecae and a well-sclerotised ventral receptacle.

Biology and immature stages

Aquatic and semi-aquatic habitats are typical for this family, although several genera have evolved structural and behavioural modifications that adapt them to remarkably divergent habitats. One of these evolutionary specialisations is the adaptation to extremes in saline concentrations. Although many shore flies frequent the muddy margins of freshwater environments, their abundance and/or biotic importance do not compare to those occurring in maritime marshes, tidal salt pools (Simpson 1976*a*: 472), or the saline and alkaline lakes of arid regions. The relative isolation and reduced interspecific competition in such habitats have resulted in the evolution of highly distinctive and specialised genera and species.

Eggs are deposited singly or in groups over the substrate (surface of algae, rocks, vegetation and the surface of plants). Oviposition by a female commonly continues for 7–10 days and documented observations under laboratory conditions of time from oviposition to eclosion takes from 13–44 days, development of the egg 1–4, each of three larval instars 3–17 and the pupal stage 2–9 days.

Most shore fly larvae feed by filtering micro-organisms from the surrounding semi-liquid medium. The food sources vary considerably, depending on the feeding habits. Most larvae are microphagous on bacteria, unicellular algae and yeasts, although some prefer dead and decaying animal tissue or excrement (Foote 1995). An exception is *Ochthera*, the larval cephaloskeleton (which includes pointed mouthhooks), is robust and well-suited for piercing exoskeletons of prey. Ferrar (1987: 167) and Hennig (1943, 1952: 345) summarised data then available and the latter attempted a partial identification key.

Feeding habits of adults likewise vary considerably, but most feed on microscopic algae (Foote 1977, 1981*a*, *b*), dinoflagellates and other unicellular forms. A major digression from the microphagous feeding habit occurs in *Ochthera* (Simpson 1975). Prey of *Ochthera* varies from bloodworms, captured by excavating the substrate, to adults of most small insects that can be overpowered. Species of many other genera are polyphagous, sometimes even cannibalistic, scavenging on dead or dying insects and others feed on nectar and leaf epidermis besides having the typical microphagous habit. These habits have been reported in part (or entirely) for adults of *Hecamede* Haliday (Ardö 1957), *Hydrellia* (Deonier 1971, 1998) and *Notiphila* Fallén (Mathis 1979*a*).

Although the mating behaviour of ephydrids has been widely studied, generalisation is difficult. Dahl (1959) distinguished six phases while studying the mating behaviour of Scandinavian shore flies. Deonier (1971) found it more flexible simply to recognise courtship and mating behaviour for describing the mating habits of various *Hydrellia* species.

The basic work on shore fly ecology is Dahl's (1959) study of the Scandinavian fauna. Other papers since then include Collins (1975), Deonier (1965), Foote (1995) and Simpson (1976*b*). The publications by Scheiring & Foote (1973) and Simpson (1976*b*) provide excellent summaries for several species and more extensive information on the biology of immature stages is found in the works of Foote (1995), Simpson (1976*a*: 469), Wirth *et al*. (1987: 1028) and Zatwarnicki (1997: 384). Oldroyd (1964: 189) aptly summarised shore fly biology, when he wrote: "Evidently we are seeing in the Ephydridae a family of flies in the full flower of its evolution, and as such they offer attractive material for study, not only to the dipterist, but also to students of insect physiology and behaviour".

Economic significance

Ephydridae, or shore flies, are mainly beneficial, providing food for wildlife, especially waterfowl that inhabit the marshes where these flies so commonly breed. In a few areas, however, the leaf- or stem-mines of *Hydrellia* become extensive enough to damage crops of watercress, rice, barley and other irrigated cereals (Grigarick 1959). Lange *et al*. (1953) estimated that *H. griseola* (Fallén, 1813) destroyed 10–20% of the Californian rice crop in 1953. More recently, Mathis *et al*. (2006) reported on *H. wirthi* Korytkowski, 1982, which is an invasive pest on rice in South America and now in the south-eastern United States. A species of *Notiphila* was also reported to damage the roots of rice in Japan (Koizumi 1949).

Classification

The family Ephydridae is mostly delimited herein to Chandler's (1987) characterisation and does not include the subfamily Nannodastinae and genus *Diastata* Meigen (see Chapter 104). One departure from Chandler, is the inclusion of the tribe Risini (formerly a separate family, Risidae). The family is divided into five subfamilies: Discomyzinae, Ephydrinae, Gymnomyzinae, Hydrelliinae and Ilytheinae (Zatwarnicki 1992). The most homogeneous subfamily is Discomyzinae, comprising three tribes: Discomyzini, Psilopini and Risini. The sister-group of Discomyzinae is Hydrelliinae, which is divided into five tribes: Atissini, Dryxini, Hydrelliini, Notiphilini and Typopsilopini. Of the remaining three subfamilies, Gymnomyzinae is the most diverse, having six tribes: Discocerinini, Gastropini, Gymnomyzini, Hecamedini, Lipochaetini and Ochtherini. Only two tribes, Hyadinini and Ilytheini, comprise the subfamily Ilytheinae. The sister-group of Ilytheinae is the most synapomorphic subfamily, Ephydrinae and includes four tribes: Dagini, Ephydrini, Parydrini and Scatellini.

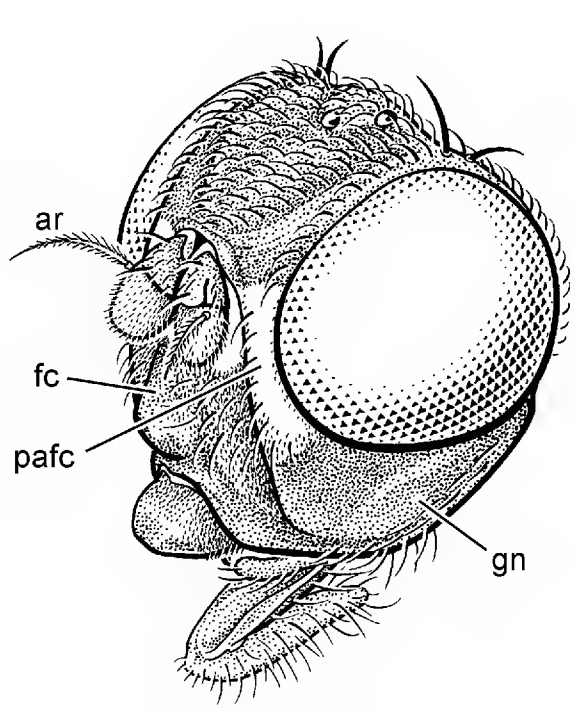
Within the family, several recent papers have substantially clarified the phylogenetic relationships at the generic level within a tribe. These include the following papers: Mathis & Zatwarnicki (2002, Dryxini); Mathis & Zatwarnicki (2007, Notiphilini); Zatwarnicki & Hagenlund (2017, Gastropini); Zatwarnicki & Mathis (2012, Lipochaetini); Zatwarnicki & Ryczko (2014, Hyadinini); Zatwarnicki *et al*. (2016*b*, Discocerinini); and Zhang *et al*. (2005, Dagini, in part).

The current classification differs considerably from those used in various regional catalogues (including the Afrotropical Region by Cogan 1980), being supported predominantly by characters of the male terminalia. The previous classification with four subfamilies was based on thoracic setation and

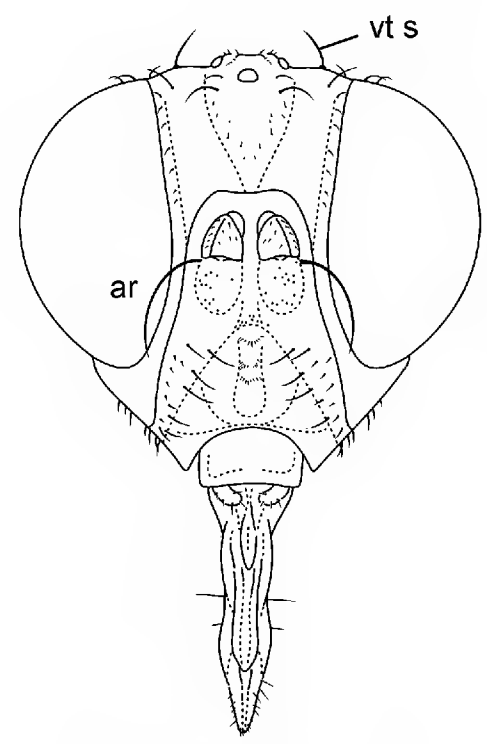
conformation of the face and was proposed by Ezra T. Cresson, Jr. during the years 1942–1949. Mathis (1991: 210), Mathis & Zatwarnicki (1995: 3) and Zatwarnicki (1992) published brief histories on the development of shore fly classifications.

Almost 2,000 species of Ephydridae are known globally and are grouped into 130 genera (Mathis & Zatwarnicki 1995: 21 and updates), from which 379 species in 69 genera are known from the Afrotropical Region. All shore fly tribes (20) are widespread geographically and are represented in the Afrotropics. Many species occur in two or more zoogeographical regions and a few are virtually cosmopolitan: *Discocerina obscurella*, *Hydrellia griseola* and *Scatella stagnalis* (Fallén, 1813).

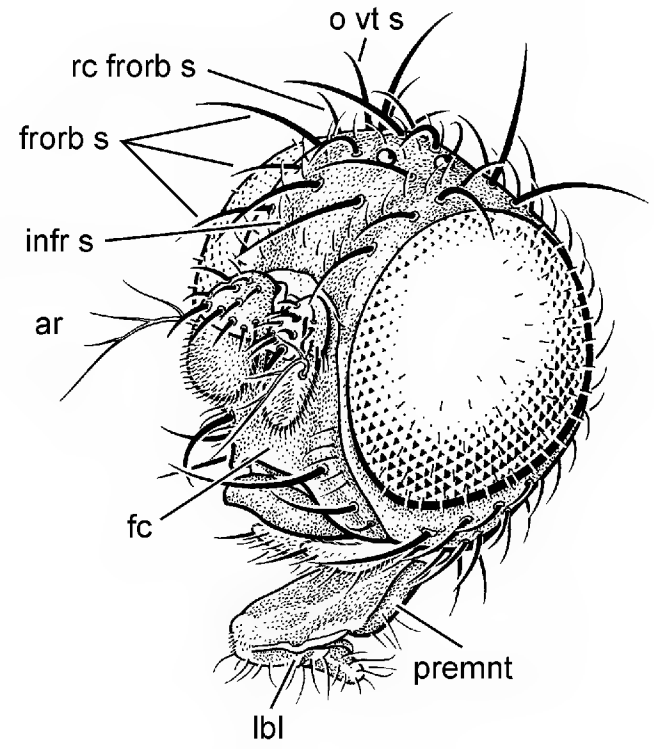
Although not directly germane to the below identification key, a few comments are appropriate on the position of the



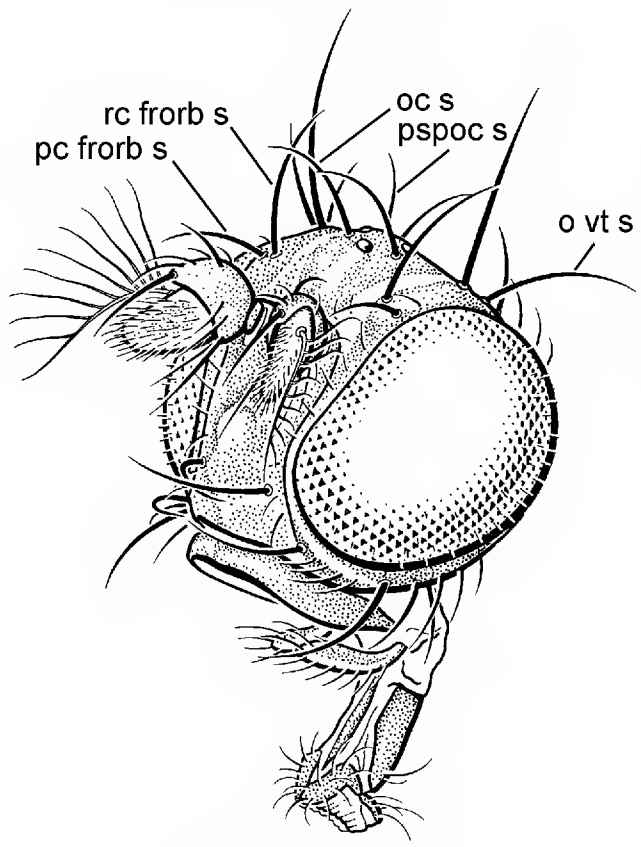
30 *Mosillus*



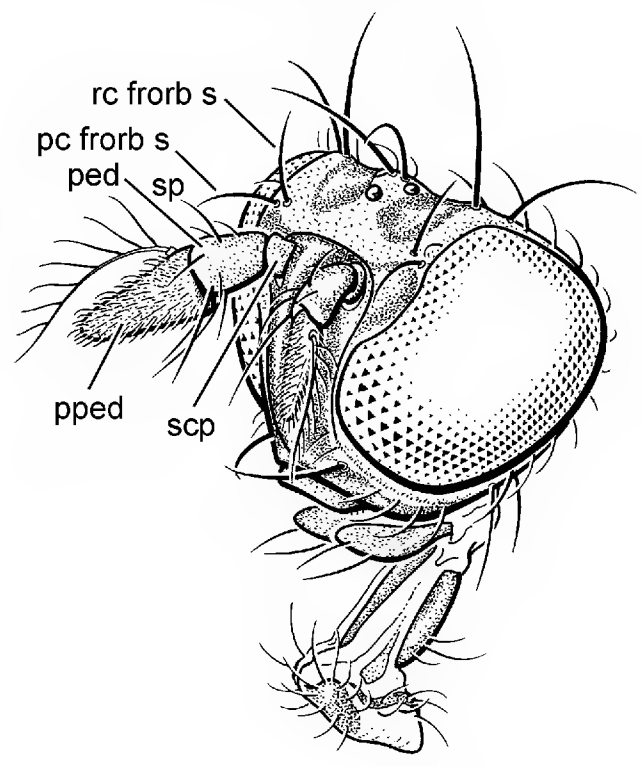
31 *Placopsidella*



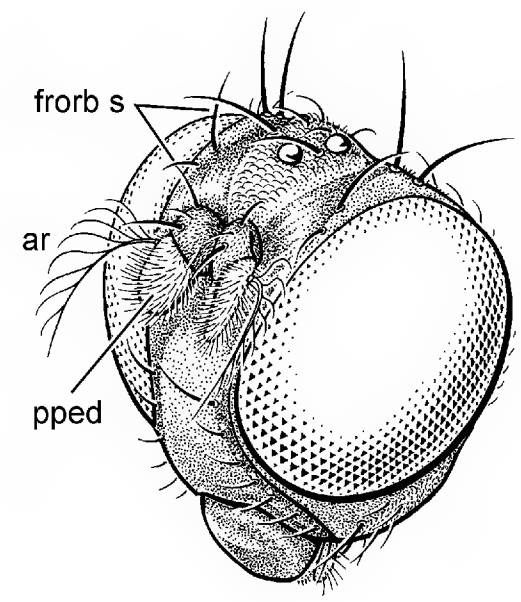
32 *Paratissa*



33 *Clasiopella*



34 *Ceropsilopa*

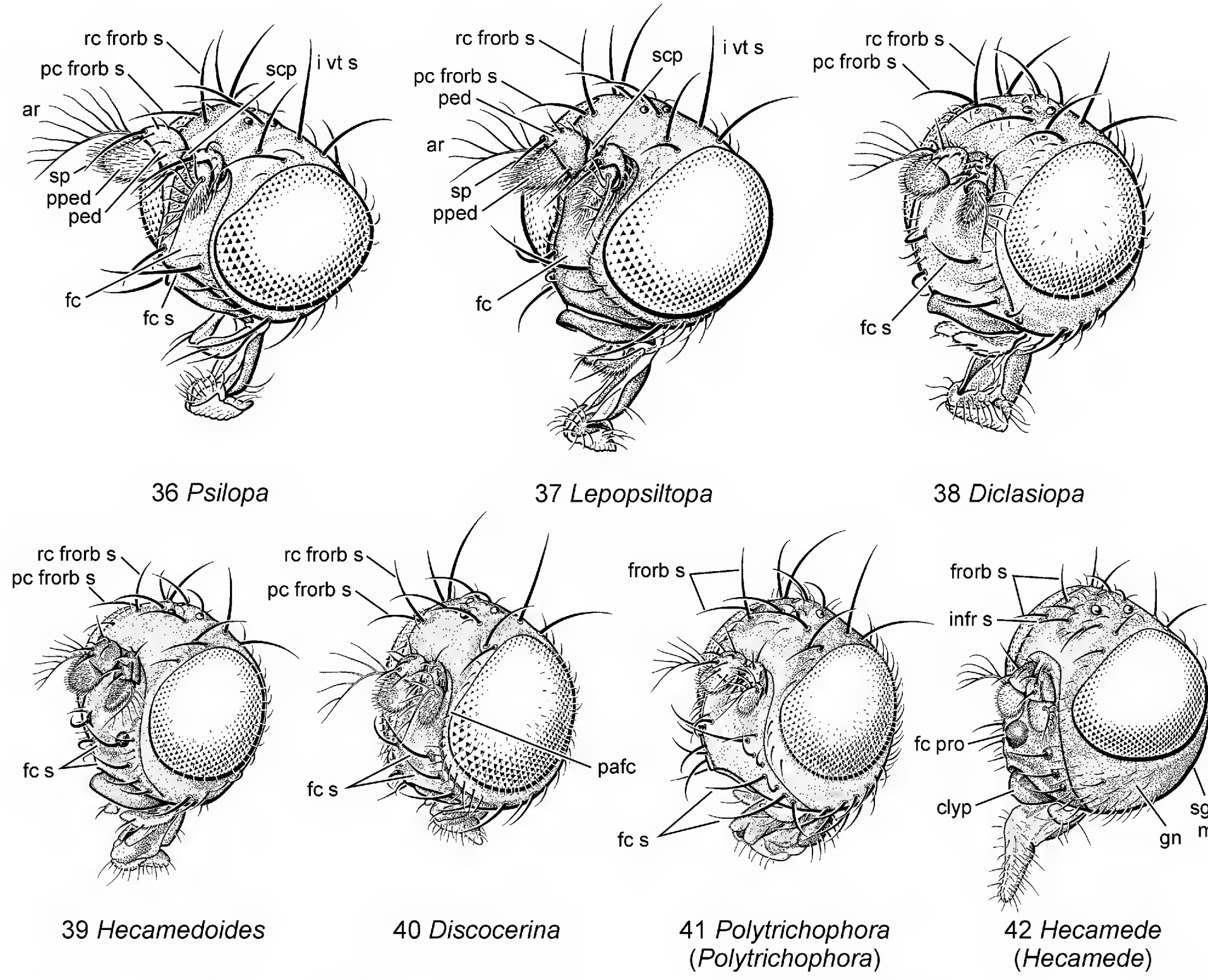


35 *Athyroglossa* (*Athyroglossa*)

Figs 100.30–35. Heads of Ephydridae (all non-Afrotropical): (30) *Mosillus tibialis* Cresson, anterolateral view; (31) *Placopsidella phaeonotata* Mathis, frontal view; (32) *Paratissa semilutea* (Loew), anterolateral view; (33) same, *Clasiopella uncinata* Hendel; (34) same, *Ceropsilopa coquilletti* Cresson; (35) same, *Athyroglossa* (*Athyroglossa*) *glaphyropus* Loew. Figs 30, 32–35 (Wirth *et al*. 1987, figs 27, 6, 14, 13, 4, respectively), Fig. 31 (after Mathis 1986*a*, fig. 17).

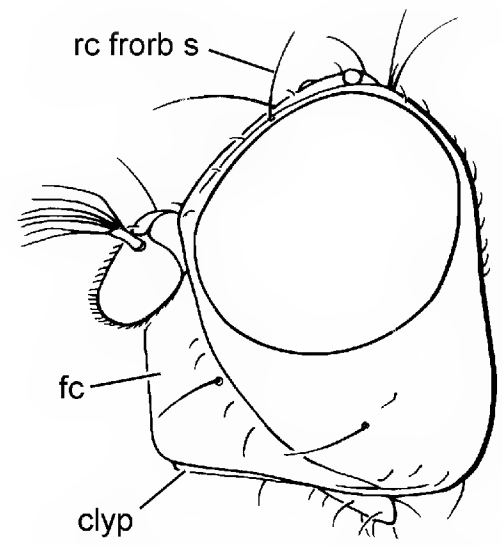
Abbreviations: ar – arista; fc – face; frorb s – fronto-orbital setae; gn – gena; infr s – interfrontal seta; lbl – labellum; o vt s – outer vertical seta; oc s – ocellar seta; pafc – parafacial; pc frorb s – proclinate fronto-orbital seta; ped – pedicel; pped – postpedicel; premnt – prementum; pspoc s – pseudopostocellar seta; rc frorb s – reclinate fronto-orbital seta; scp – scape; sp – spine; vt s – vertical seta.

family within the superfamily Ephydroidea (= Drosophiloidea of earlier authors). Several authors have dealt with the classification of the so-called "acalyptrate" Diptera, but here the discussion is limited to the past few decades, beginning with Hennig (1958, 1971), who first employed cladistic methods. Hennig's first attempt (1958) characterised the Ephydroidea and included the following families: Camillidae, Curtonotidae, Diastatidae, Drosophilidae and Ephydridae. With minor modification, these families have remained the principal players, indicating that the superfamily is relatively well-characterised and represents a monophyletic lineage. Hennig (1958) identified the family Camillidae as the sister-group to the Ephydridae, based on the shared reduction or loss of the anal cell (= cell *cua*) and vein (= vein *CuA+CuP*). Hennig further suggested that the family Diastatidae is the sister-group to a combined Ephydridae + Camillidae lineage, as all these taxa lack abdominal spiracle 7. In 1971, however, Hennig concluded that the Camillidae were not the sister-group, primarily based on a long and narrow dorsolateral projection of the antennal postpedicel, a putative synapomorphy that is shared with Drosophilidae and the genus *Curtonotum* Macquart (Curtonotidae). Hennig divided the superfamily into two basal lineages, the Drosophilidea (Camillidae, Curtonotidae and Drosophilidae) and the Ephydridea (Diastatidae and

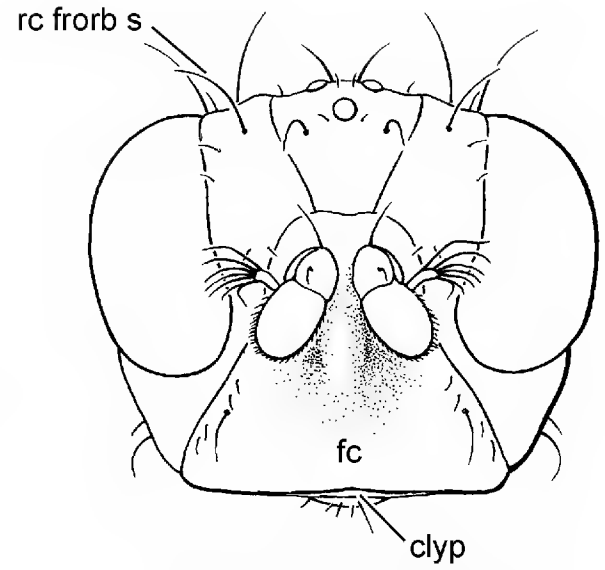


Figs 100.36–42. Heads of Ephydridae (all anterolateral views; non-Afrotropical): (36) *Psilopa flavida* Coquillett; (37) *Leptopsilopa varipes* (Coquillett); (38) *Diclasiopa lacteipennis* (Loew); (39) *Hecamedoides unisetosus* (Collin); (40) *Discocerina obscurella* (Fallén); (41) *Polytrichophora* (*Polytrichophora*) *agens* Cresson; (42) *Hecamede* (*Hecamede*) *albicans* (Meigen). Figs 36–42 (Wirth *et al*. 1987, figs 15, 12, 17, 18, 10, 8, 19, respectively).

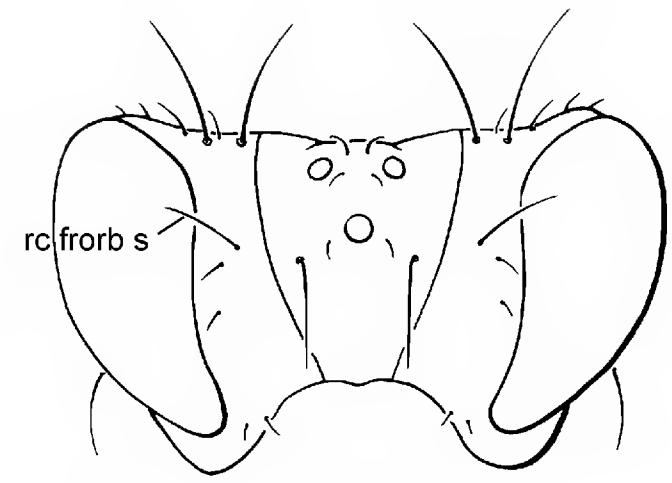
Abbreviations: ar – arista; clyp – clypeus; fc – face; fc pro – facial prominence; fc s – facial setae; frorb s – fronto-orbital setae; gn – gena; i vt s – inner vertical seta; infr s – interfrontal seta; pafc – parafacial; pc frorb s – proclinate fronto-orbital seta; ped – pedicel; pped – postpedicel; rc frorb s – reclinate fronto-orbital seta; scp – scape; sgn m – subgenal margin; sp – spine.



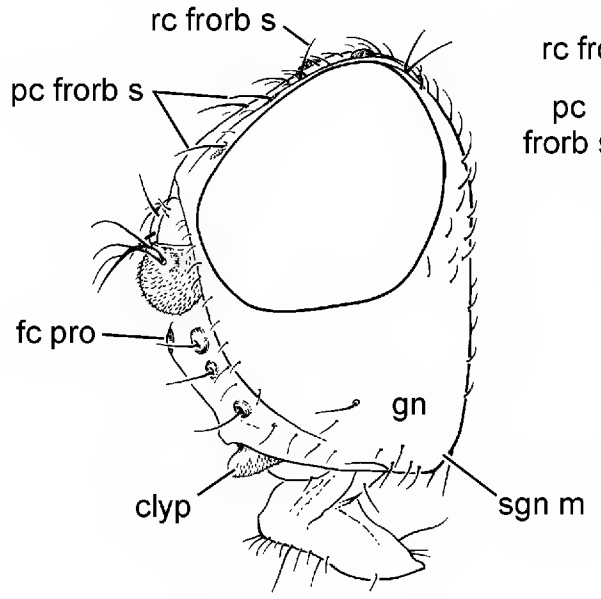
43 *Elephantinosoma*



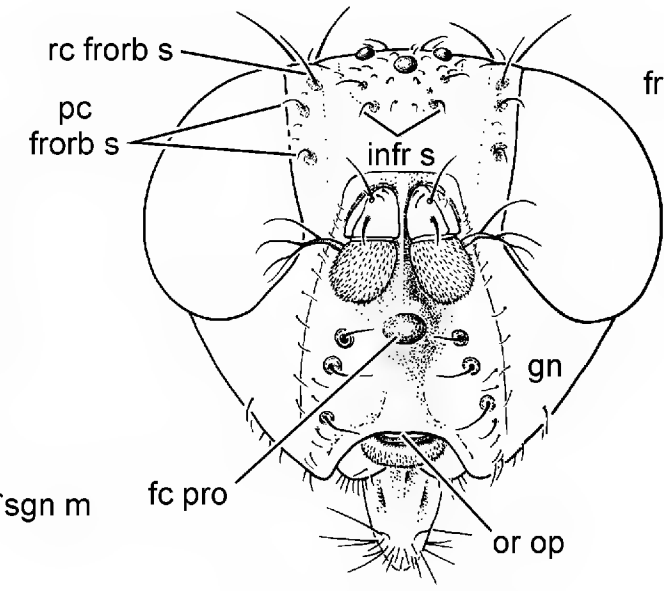
44 *Elephantinosoma*



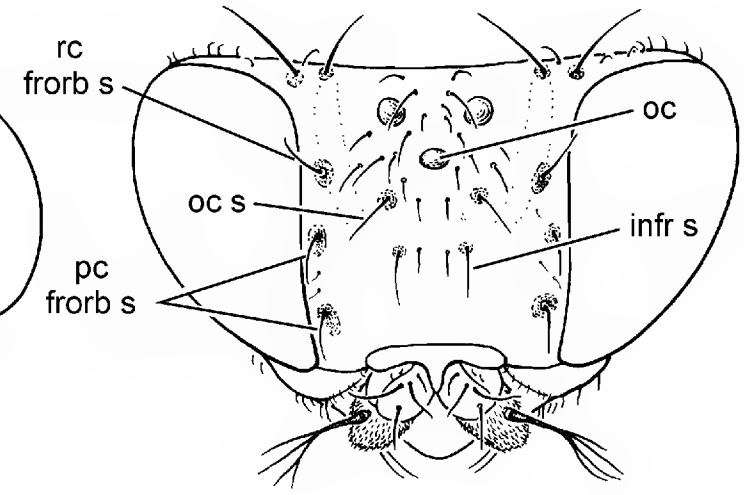
45 *Elephantinosoma*



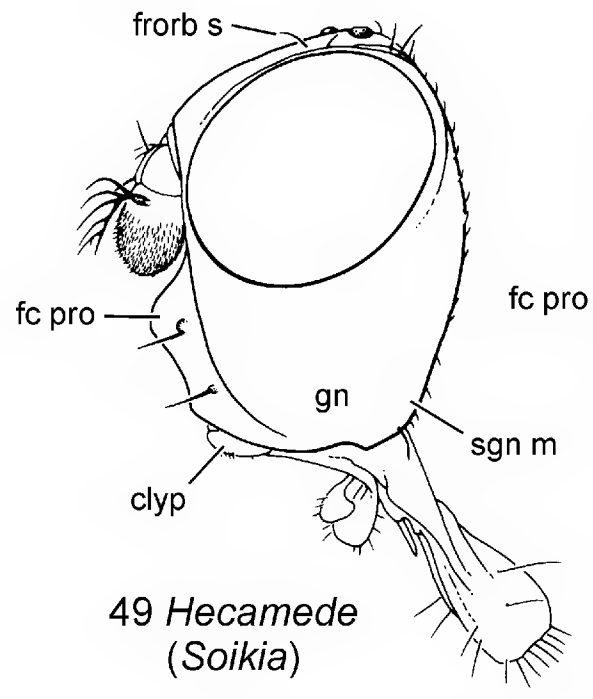
46 *Hecamede* (*Hecamede*)



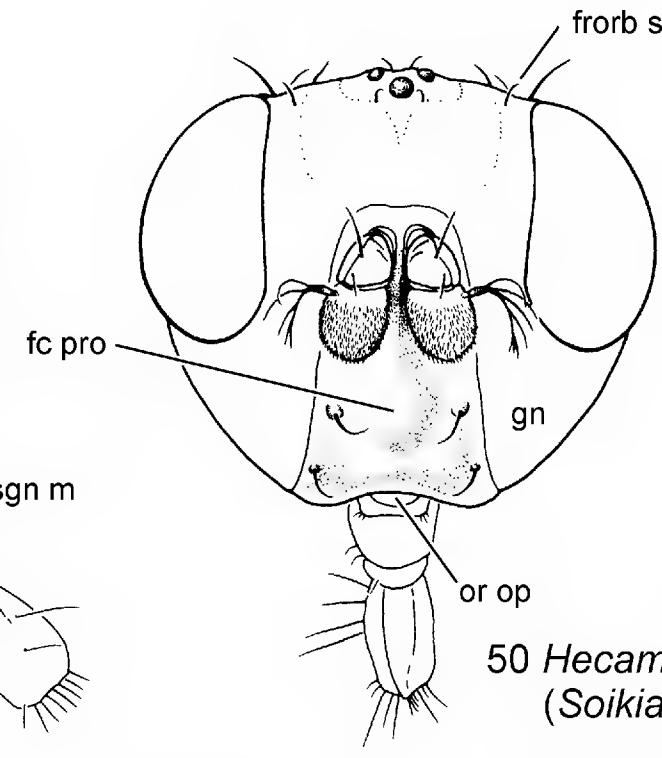
47 *Hecamede* (*Hecamede*)



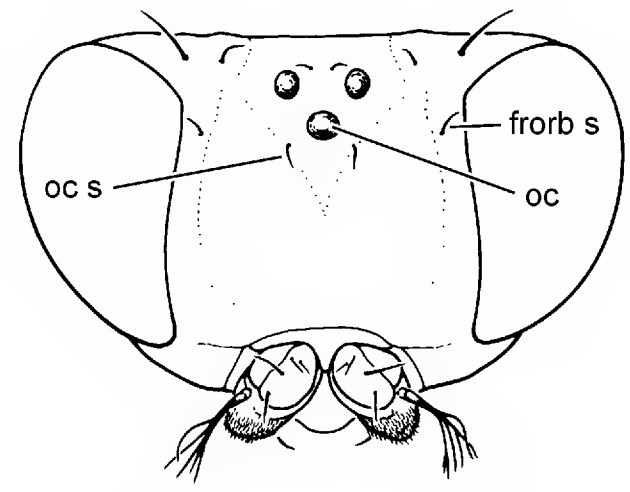
48 *Hecamede* (*Hecamede*)



49 *Hecamede* (*Soikia*)



50 *Hecamede* (*Soikia*)



51 *Hecamede* (*Soikia*)

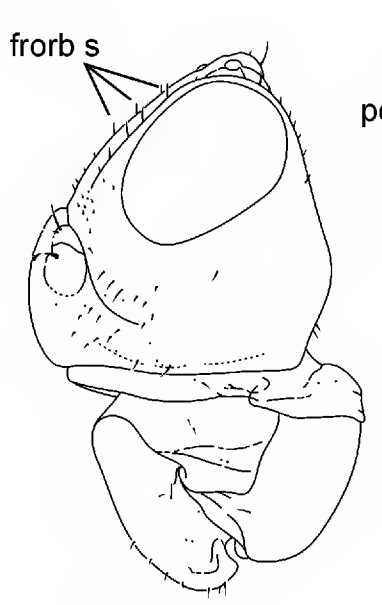
Figs 100.43–51. Heads of Ephydridae: (43) *Elephantinosoma chnumi* Becker, lateral view; (44) same, frontal view; (45) same, dorsal view; (46) *Hecamede* (*Hecamede*) *brasiliensis* Cresson, lateral view; (47) same, frontal view; (48) same, dorsal view; (49) *H.* (*Soikia*) *nuda* Wirth, lateral view; (50) same, frontal view; (51) same, dorsal view. Figs 43–45 (Mathis & Deeming 1987, figs 2, 1, 3, respectively), Figs 46–50 (Mathis 1993*b*, figs 6, 5, 7, 49, 48, 50, respectively).

Abbreviations: clyp – clypeus; fc – face; fc pro – facial prominence; frorb s – fronto-orbital seta; gn – gena; infr s – interfrontal seta; oc – ocellus; oc s – ocellar seta; or op – oral opening; pc frorb s – proclinate fronto-orbital setae; rc frorb s – reclinate fronto-orbital seta; sgn m – subgenal margin.

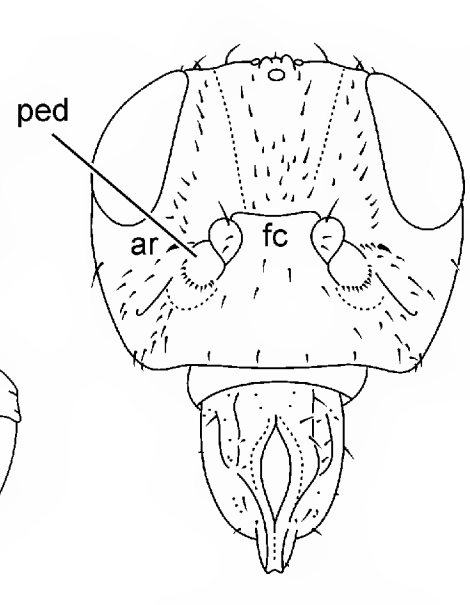
Ephydridae) and cited characters from the female terminalia, especially the female ventral receptacle and spermathecae, as evidence.

Griffiths (1972: 100), followed by Chandler (1987), next contributed to the classification. Griffiths (1972: 109) generally concurred with Hennig's classification, but restricted Diastatidae to the genus *Diastata*, which he included in the family Ephydridae and proposed the family Campichoetidae for *Campichoeta* Macquart and *Euthychaeta* Loew. Chandler (1987) restudied the evidence, providing additional details on *Campichoeta*, *Euthychaeta* and several genera of Drosophilidae and commenting on the family Risidae (Papp 1977), which is here included in the family Ephydridae. Chandler's study of these taxa was presented in part as a matrix of data and taxa, similar to those produced by Hennig and Griffiths, and like these, lacked an explicit analysis of the data.

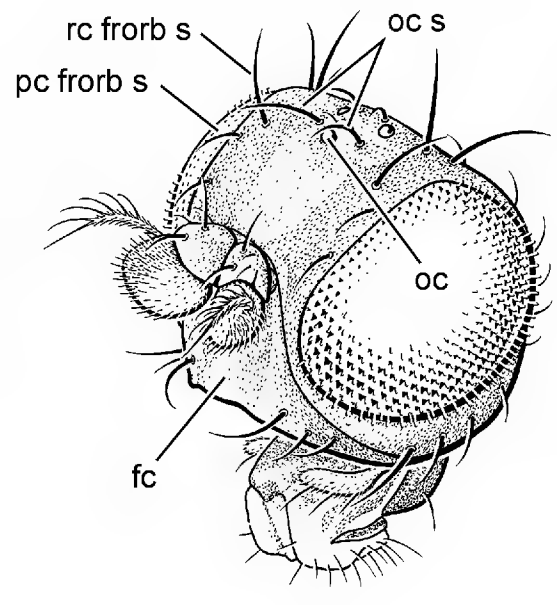
Grimaldi (1990) subjected the character data of Chandler, Griffiths and Hennig (18 characters), plus discoveries of his own (2 characters), to the computerised algorithm PAUP®, which generated three equally parsimonious trees. Although differing in the lineages immediately related to Drosophilinae and Steganinae, there was stability in the families closely



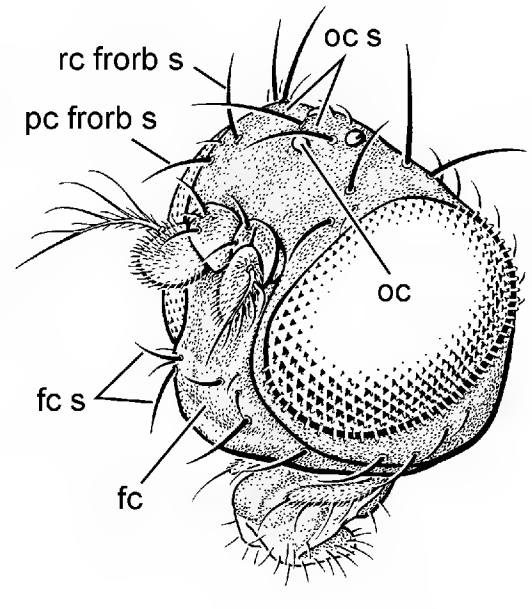
52 *Asmeringa*



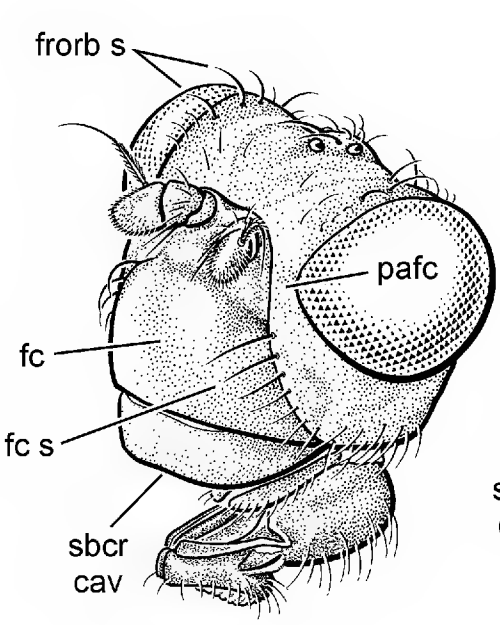
53 *Asmeringa*



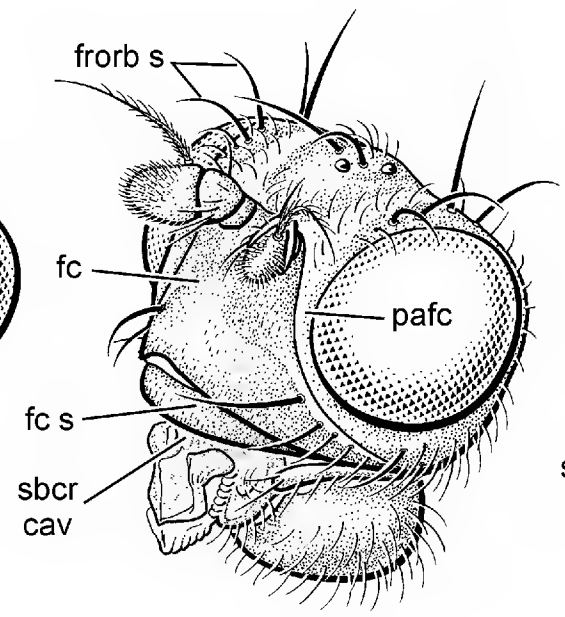
54 *Atissa*



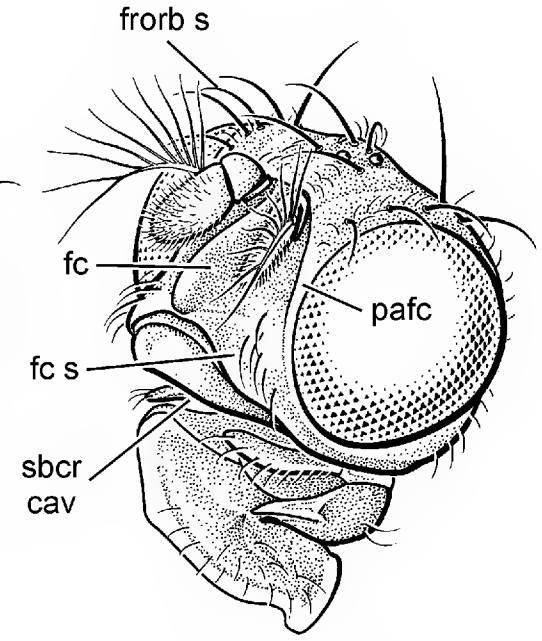
55 *Ptilomyia*



56 *Parydra* (*Parydra*)



57 *Parydra* (*Chaetoapnaea*)



58 *Brachydeutera*

Figs 100.52–58. Heads of Ephydridae: (52) *Asmeringa inermis* Becker, lateral view; (53) same, frontal view; (54) *Atissa pygmaea* (Haliday), anterolateral view (non-Afrotropical); (55) same, *Ptilomyia mabelae* (Cresson) (non-Afrotropical); (56) same, *Parydra* (*Parydra*) *aquila* (Fallén) (non-Afrotropical); (57) same, *Parydra* (*Chaetoapnaea*) *fossarum* (Haliday) (non-Afrotropical); (58) same, *Brachydeutera argentata* (Walker) (non-Afrotropical). Figs 52, 53 (after Mathis 1984*a*, figs 13, 14), Figs 54–58 (Wirth *et al*. 1987, figs 22, 20, 33, 34, as *Parydra parasocia*, 2, respectively).

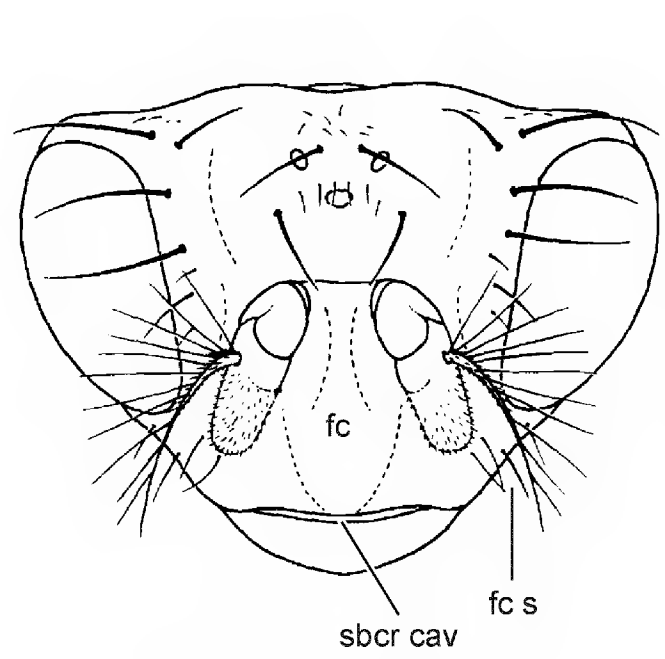
Abbreviations: ar – arista; fc – face; fc s – facial setae; frorb s – fronto-orbital seta(e); oc – ocellus; oc s – ocellar setae; pafc – parafacial; pc frorb s – proclinate fronto-orbital seta; ped – pedicel; rc frorb s – reclinate fronto-orbital seta; sbcr cav – subcranial cavity.

related to Ephydridae. The family Risidae was identified as the sister-group to Ephydridae and these two families, in turn, were the sister-group to Camillidae. The family Diastatidae *sensu stricto*, was the sister-group to the assemblage comprising Camillidae, Ephydridae and Risidae.

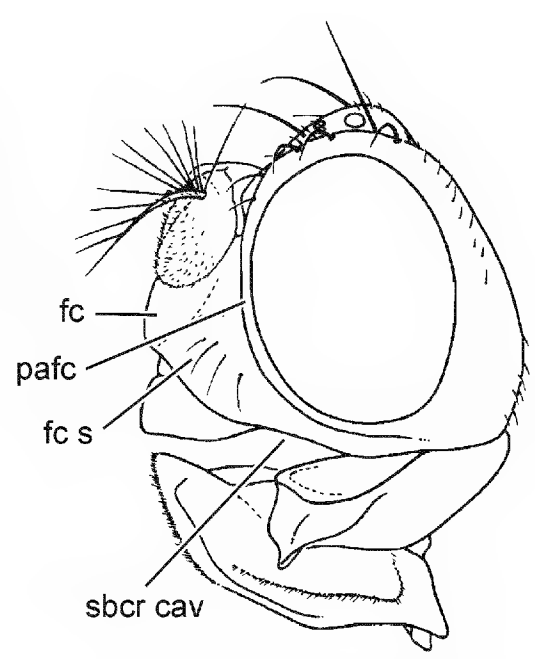
More recently, in an analysis of molecular data, Wiegmann *et al.* (2011) recovered the superfamily Ephydroidea and further suggested its unique placement as the sister-group to Calyptratae. The family Ephydridae was recovered as sister-group to the remaining six families in this superfamily, which also included Braulidae and Cryptochetidae. The last two named families are enigmatic and highly derived groups of insect parasites, which were recovered as a monophyletic lineage and as the sister-group of Drosophilidae.

Identification

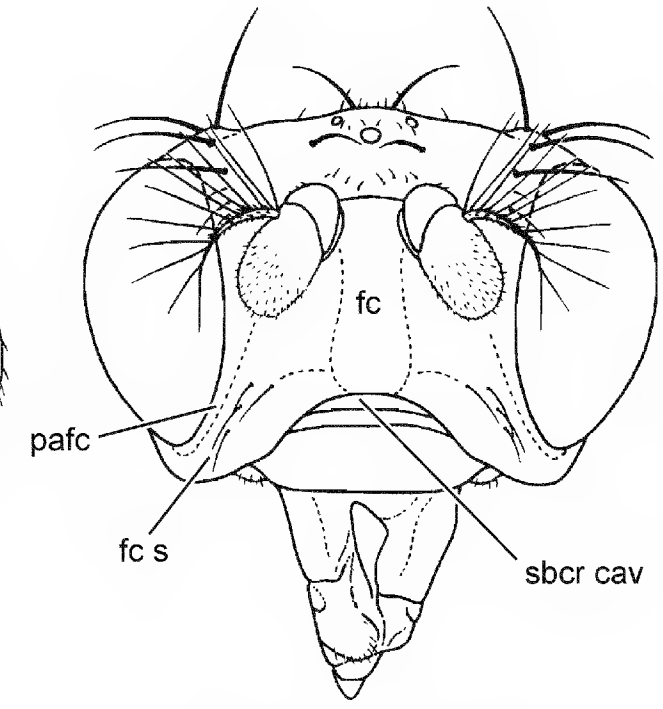
There is currently no identification key to genera on a global basis. References to existent identification keys to species are found in Mathis & Zatwarnicki's (1995: 21 and updates) world catalogue. Although unfinished, Cresson (1946, 1947) began a series of synopses on the Afrotropical shore flies that included identification keys to species. Ephydridae are best micro-pinned in the field for later double-mounting (see Chapter 2).



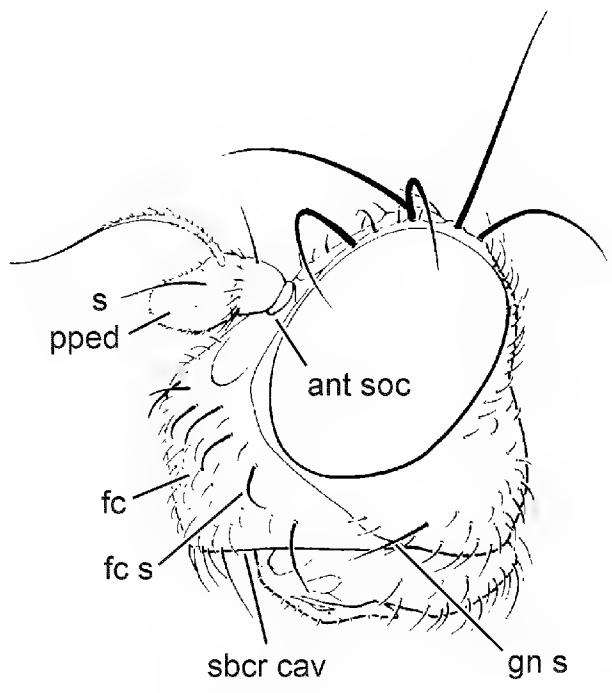
59 *Brachydeutera*



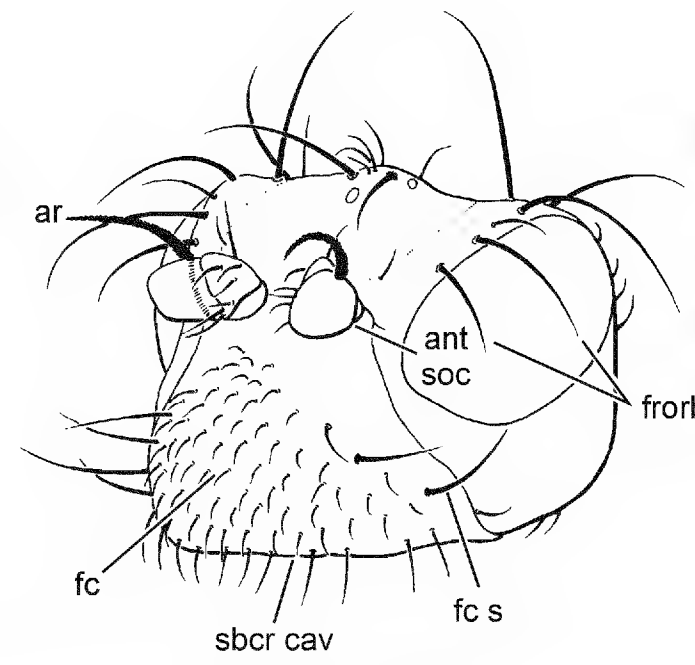
60 *Brachydeutera*



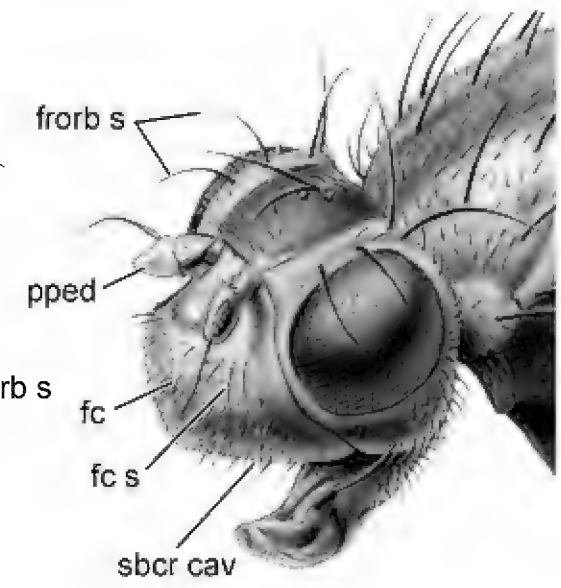
61 *Brachydeutera*



62 *Setacera*



63 *Haloscatella*



64 *Neoephydra*

Figs 100.59–64. Heads and head and thorax of Ephydridae: (59) head of *Brachydeutera meridionalis* (Rondani), dorsal view; (60) same, lateral view; (61) same, frontal view; (62) same, *Setacera multicolor* (Giordani Soika), lateral view; (63) same, *Haloscatella salinaria* (Sturtevant & Wheeler), frontolateral view (non-Afrotropical); (64) head and thorax of *Neoephydra araucaria* Mathis, frontolateral view (non-Afrotropical). Figs 59–61 (Mathis & Ghorpadé 1985, figs 14, 12, 13, respectively), Fig. 62 (Mathis 1982, fig. 30), Fig. 63 (Mathis 1979*b*, fig. 22), Fig. 64 (Mathis 2008, fig. 11).

Abbreviations: ant soc – antennal socket; ar – arista; fc – face; fc s – facial setae; frorb s – fronto-orbital setae; gn s – genal seta; pafc – parafacial; pped – postpedicel; s – seta; sbcr cav – subcranial cavity.

Key to genera of Afrotropical Ephydridae

1. Head with fronto-orbital setae reclinate and proclinate or absent (e.g., Figs 7–9, 14, 15, 18–26, 32–55, 65–71, 73–77, 80, 84–90); medial facial area and lower facial margin without setae; if costal wing vein (C) only extends to vein R_{4+5}, then shaft of mid tibia with strong dorsal setae, or wing without alula, or proboscis long and geniculate; facial setae inserted in more or less vertical series, parallel with parafacial setae; subcranial cavity small to large 2

– Head with fronto-orbital setae lateroclinate, usually conspicuous (e.g., Figs 56–61, 63, 64, 92–95); medial facial area and lower facial margin setose, the latter often with long setae, if bare, then costal wing vein (C) short, extended to vein R_{4+5}, but without strong dorsal setae on mid tibia, or subcranial cavity large, with prominent clypeus, large mouthparts and antennal arista at most short-plumose (Figs 56, 57); insertions of facial series of setae convergent above; subcranial cavity large and cavernous (EPHYDRINAE) 68

2. Thorax with presutural or sutural dorsocentral seta conspicuous (e.g., Figs 66, 71, 96, 98); if without this seta, then hind femur as long as or longer than abdomen (Fig. 1); or head and thorax as in Fig. 70 (only 1 notopleural seta, antennal arista pectinate, face flat without carina at mouth edge or between antennae and without distinct ocellar or fronto-orbital setae); or 2 well-developed pairs of postsutural dorsocentral setae and no acrostichal setae (e.g., Fig. 65) 3

– Thorax without presutural or sutural dorsocentral seta or inconspicuous (e.g., Figs 99–101); other characters not as above 21

3. Thorax with posterior notopleural seta inserted conspicuously above level of anterior seta (as in Fig. 104) (ILYTHEINAE [in part]) 4

– Thorax with posterior notopleural seta inserted at same level as anterior seta (as in Fig. 103) (HYDRELLIINAE [in part]) 8

4. Head with fronto-orbital setae greatly reduced, at most with tiny proclinate setulae (e.g., Fig. 7) (HYADININI [in part]) 5

– Head with fronto-orbital setae well-developed (e.g., Figs 9, 66) (ILYTHEINI) 6

5. Antennal arista bearing conspicuous dorsal branches, length of branches much longer than basal aristal width (Fig. 65); thorax with 2 dorsocentral setae, both postsutural (0 + 2) . . . . . *Nostima* Coquillett

– Antennal arista appearing bare, length of dorsal branches less than basal aristal width (Fig. 7); thorax with 2 dorsocentral setae, anterior seta presutural or sutural (1 + 1) . . . . . *Philygria* Stenhammar

6. Thorax with 3 dorsocentral setae (1 + 2) . . . . . *Donaceus* Cresson

– Thorax with 2 dorsocentral setae (1 + 1) 7

7. Wing vein R_{2+3} long, subparallel to costal vein (C); costal section 2 over twice section 3 (Fig. 105) . . . . . *Ilythea* Haliday

– Wing vein R_{2+3} short, running almost straight to costal vein (C); costal section 2 subequal to section 3 (Fig. 106) . . . . . *Zeros* Cresson

8. Compound eye bearing short, dense setulae; ocellar setae seldom as strong as pseudopostocellar setae, usually much weaker (Fig. 10); thorax with postsutural supra-alar seta usually short, not longer than posterior notopleural seta (Fig. 96) (HYDRELLIINI) . . . . . *Hydrellia* Robineau-Desvoidy

– Compound eye bare; ocellar setae stronger than weak pseudopostocellar setae, or reduced (e.g., Figs 14–26, 67–71); thorax with postsutural supra-alar seta longer than posterior notopleural seta 9

9. Mid tibia without dorsal, spine-like setae; usually shiny black to dark green species (TYPOPSILOPINI) 10

– Mid tibia with 1–4 erect, spine-like setae along dorsal surface (e.g., Fig. 115); usually dull, micro-tomentose species 11

10. Body generally micro-tomentose; head with frons and thorax with mesonotum with micro-tomentose vittae; paravertical seta well-developed, inclinate (Fig. 69); thorax with 4 dorsocentral setae (1 + 3), anterior two setae shorter than posterior two setae; wing membrane yellowish hyaline . . . . . *Psilopoidea* Cresson

– Body, especially dorsum, shiny black or dark green, sparsely micro-tomentose; head with frons and thorax with mesonotum without micro-tomentose vittae; paravertical seta very weakly developed or absent (Fig. 68); thorax with 3 dorsocentral setae (1 + 2), first seta as long as second seta; wing membrane greyish hyaline . . . . . *Typopsilopa* Cresson

11. Costal wing vein (*C*) extended to vein R_{4+5} (e.g., Fig. 107); thorax with 3 dorsocentral setae (1 + 2) (NOTIPHILINI). . . . . *Notiphila* Fallén *sensu lato* 12

– Costal wing vein (*C*) extended to vein M_1 (as in Fig. 108); thorax with 4 dorsocentral setae (1 + 3) or 1 (0 + 1) (DRYXINI) 13

12. Head with 2 small, proclinate fronto-orbital setae inserted laterad to large, reclinate fronto-orbital seta; mid tibia bearing 4 erect setae along dorsum; fore coxa with 2 distinctly larger setae on lower ½ of anterolateral margin; male mid femur without posteroventral comb of setae . . . . . *Notiphila* (*Agrolimna* Cresson)

– Head with 0–1 small, proclinate fronto-orbital setae inserted laterad to large, reclinate fronto-orbital seta (Fig. 67); mid tibia bearing 3 erect setae along dorsum (Fig. 115); fore coxa without distinctly larger setae on lower ½ of anterolateral margin; male mid femur bearing row of comb-like setae along posteroventral margin (Fig. 115) . . . . . *Notiphila sensu stricto*

13. Thorax with notopleuron bearing 1 large seta; without presutural supra-alar seta (e.g., Fig. 97); mid and hind femora usually moderately long to very long, length subequal to that of abdomen 14

– Thorax with notopleuron bearing 2 large setae; with presutural supra-alar seta (absent in one species of *Oedenops* Becker) (e.g., Fig. 98); mid and hind femora normally developed, length much shorter than that of abdomen 16

14. Head with ocellar setae, although short, inserted slightly in front of anterior ocellus; with reclinate fronto-orbital seta (Figs 14, 15); thorax with anepisternum with 1 well-developed seta along posterior margin; wing vein R_1 bare along dorsum; stem vein without setulae; crossvein *dm–m* normally developed, virtually straight, forming acute inner angle with vein M_1 . . . . . *Corythophora* Loew

– Head without ocellar setae; without reclinate fronto-orbital seta (e.g., Figs 16, 17, 70); thorax with anepisternum with 2 or 3 thin, long, setulae-like setae along posterior margin; wing vein R_1 bearing several setulae along dorsum; stem vein basad to humeral crossvein, bearing several pale, thin setulae on ventral surface; crossvein *dm–m* moderately long to long, sinuous 15

15. Antennal arista bearing 12 or more long, dorsal branches (Figs 16, 17); thorax with katepisternum bearing row of slender setae near-dorsal margin; katepisternal seta usually well-developed (secondarily reduced or absent in some species); wing crossvein *dm–m* sinuous, long, generally running parallel; mid and hind femora elongate, subequal to length of abdomen . . . . . *Dryxo* Robineau-Desvoidy

– Antennal arista bearing 7–9 long, dorsal branches (Fig. 70); katepisternum without row of slender setae along dorsal margin; katepisternal seta reduced; wing crossvein *dm–m* shallowly sinuous, generally forming angle with adjacent margin of wing; mid and hind femora normally developed, much shorter than length of abdomen. . . . . *Omyxa* Mathis & Zatwarnicki

16. Thorax without katepisternal seta or this very weakly developed; antennal arista with 3–6 long branches along dorsal surface . . . . . *Oedenops* Becker

– Thorax with katepisternal seta usually well-developed (sometimes pale); antennal arista with 6 or more long branches along dorsal surface 17

17. Head with 2–3 long facial setae, length subequal to combined length of antennal pedicel and postpedicel, if 2 setae present, then these well-separated, dorsal seta at about mid height, ventral seta closer to oral margin than dorsal seta (Figs 22, 23); stem wing vein bearing 1–3 (usually 2) setulae on dorsum . . . . . *Oedenopiforma* Cogan

– Head with 1 long facial seta, if larger setae present, then these not as long or as separated as above, usually arranged in somewhat vertical series of short setulae (e.g., Figs 18, 19, 24, 25, 71); stem wing vein without setulae. 18

18. Fore femur with anteroventral row of very short, stout, tooth-like setae; bearing 4–5 long setae along apical ½ of posteroventral surface, length approaching 2 × width of femur; head with proclinate fronto-orbital setae greatly reduced and subequal, setula-like (Figs 18, 19); face, gena, anepisternum, anterior surface of tibiae and basolateral surface of scutellum densely, silvery micro-tomentose. . . . . *Afrolimna* Cogan

– Fore femur without row of closely set, very short, somewhat blunt, tooth-like spines along anteroventral surface; without long setae as above; head with anterior proclinate fronto-orbital seta larger than posterior proclinate seta (Figs 24–26); face, *etc.*, not silvery micro-tomentose in above combination . . . . . *Paralimna* Loew *sensu lato* 19

19. Head with gena high, height *ca* ⅓ or more or eye height; antennal postpedicel short, length at most 1.5 × width (Fig. 71) . . . . . *Paralimna sensu stricto*

– Head with gena short, height *ca* ¼ eye height; antennal postpedicel elongate, length > 2 × width (e.g., Figs 24, 25) 20

20. Thorax with scutum brown medially and through dorsocentral track, between yellowish to brownish grey margins and anepisternum brown dorsally and ventrally, grey between conspicuous vittae; wing crossvein *dm–m* and sometimes adjacent veins, with "halo" of brown . . . . . *Paralimna* (*Coganolimna* Ale-Rocha & Mathis)

– Thorax with scutum and anepisternum mostly unicolourous and greyish brown to black; wing crossvein *dm–m* and veins essentially unicolourous . . . . . *Paralimna* (*Phaiosterna* Cresson)

21. Antennal arista longer than postpedicel, bare to micro-pubescent, if pectinate, then branches short, at most 2 × aristal width at base (e.g., Figs 27–29, 76); proboscis normal. 22

– Antennal arista pectinate, with branches sometimes pale and difficult to discern (e.g., Figs 32–37, 80–83, 85), if not pectinate, then proboscis very long and geniculate (e.g., Fig. 79), or arista reduced to basal stub (e.g., Fig. 87) 30

22. Thorax with posterior notopleural seta inserted at much higher level than anterior seta (as in Fig. 104); if only posterior notopleural seta present, then this well-removed from notopleural suture, lying *ca* half-way between notopleural suture and apex of notopleuron 23

– Thorax with posterior notopleural seta inserted near ventral margin, at same level as anterior seta (as in Fig. 103); if only posterior notopleural seta present, this inserted proximal to notopleural suture, at posteroventral angle of notopleuron. 24

23. Compound eye pyriform, distinctly narrowed ventrally (Fig. 29). . . . . *Glenanthe* Haliday

– Compound eye generally oval or round, not distinctly narrowed ventrally (Fig. 8). . . . *Hyadina* Haliday

24. Head with posterior margin of postgena meeting occiput at obtuse angle, broadly rounded (as in Fig. 8), with small dark setulae; body brown to dark grey, often with some subshiny areas . . . . . *Pelina* Haliday

– Head with posterior margin of postgena sharply angulate, with fine pale setulae; body extensively shiny black, although with some grey to whitish micro-tomentum on dorsum, or body largely grey or brown micro-tomentose (GYMNOMYZINAE [in part]: GYMNOMYZINI [in part]; LIPOCHAETINI [in part]). . . 25

25. Body largely grey or brown micro-tomentose 26

– Body extensively black, shiny. 27

26. Head without outer vertical seta (Fig. 31); head narrowed below, so that mouth opening is *ca* ⅓ width of head (Fig. 31); thorax with several setae in oblique row between postalar seta and base of scutellum (Fig. 100) . . . . . *Placopsidella* Kertész

– Head with outer vertical seta; mouth opening virtually full width of head (Figs 27, 28); thorax without setae between postalar seta and base of scutellum . . . . . *Homalometopus* Becker

27. Antennal arista bearing 3–9 moderately long branches along dorsal margin, length of branches considerably greater than basal aristal width (Fig. 76); wing with alula narrow . . . . . *Gymnopiella* Cresson

– Antennal arista appearing bare, any branches present short (e.g., Figs 30, 75, 77), less than basal aristal width; wing with alula wide, auriculate 28

28. Head with gena short (eye to cheek ratio: 0.20) (Fig. 75); parafacial narrow, less than width of anterior ocellus (Fig. 75); wing membrane generally faintly infuscate appearing light brown . . . . . *Mosillus* Latreille [in part]

– Head with gena high (eye to cheek ratio 0.45, or greater) (e.g., Figs 30, 77); parafacial moderately to very wide, width greater than that of anterior ocellus (e.g., Figs 30, 77); wing membrane generally appearing milky white 29

29. Head with face appearing maculate and pitted, pits with silvery grey micro-tomentum (Fig. 77); anterior surface of mid femur rounded, bare of micro-tomentum, shiny; fore femur with posteroventral margin produced ventrally to pointed ridge bearing setae . . . . . *Chlorichaeta* Becker

– Head with face micro-sculptured, but either bare or micro-tomentum in vertical fascia, not maculate (Fig. 30); mid femur with anterior surface flat, densely micro-tomentose, micro-tomentum silvery white; fore femur bearing row of stout setae along apical ½ of posteroventral margin, these not arising from pointed ridge. . . . . *Mosillus* Latreille [in part]

30. Thorax with prescutellar acrostichal setae large (subequal to posterior dorsocentral seta), inserted widely apart (distance between each subequal to that between either prescutellar and posterior dorsocentral seta on same side) and usually in front of intra-alar seta; head with reclinate fronto-orbital seta usually inserted behind larger proclinate fronto-orbital seta (e.g., Figs 33, 34, 36, 37, 81) (DISCOMYZINAE). 31

– Thorax with prescutellar acrostichal setae small (*ca* ½–⅔ length of posterior dorsocentral seta), inserted close together (distance between *ca* ½ that between either prescutellar and posterior dorsocentral seta on same side) and behind, or aligned with, intra-alar seta; or prescutellar acrostichal setae absent; head with reclinate fronto-orbital seta usually inserted slightly anterior to larger proclinate fronto-orbital seta (*e.g.*, Figs 38–40, 54, 55, 89, 90) 44

31. Head with face distinctly carinate, sometimes carina somewhat pointed (*e.g.*, Figs 78, 79); mouthparts moderately to distinctly geniculate, length of labellum equal to prementum (*e.g.*, Figs 78, 79); wing membrane often milky white; costal vein (C) short, extended to vein R_{4+5}; without crossvein *dm–m*; head with reclinate fronto-orbital seta reduced or absent (RISINI) 32

– Head with face mostly flat, or shallowly arched, lacking distinct carina (*e.g.*, Figs 32, 84); mouthparts not geniculate (slightly so in *Rhynchopsilopa* Hendel), length of labellum slightly > ½ length of prementum (*e.g.*, Fig. 32); wing membrane hyaline to lightly infuscate, sometimes with darkened base or darkened patches, usually not milky white; costal vein (C) long, extended to vein M_1; with crossvein *dm–m*; head with reclinate fronto-orbital seta well-developed, subequal to outer vertical seta (*e.g.*, Fig. 33) 33

32. Head with all 3 fronto-orbital setae (rarely 2 or 4) proclinate, small setula-like, equal or subequal in size (Fig. 78) . . . . . .*Achaetorisa* Papp

– Head with anterior fronto-orbital seta *ca* 2–3 × longer than medial fronto-orbital seta, inclinate (Fig. 79); posterior fronto-orbital seta usually reclinate, occasionally proclinate, usually as long as anterior fronto-orbital setae, occasionally as long as medial fronto-orbital seta (Fig. 79) . . . . . .*Risa* Becker

33. Thorax with postsutural supra-alar seta, size subequal to presutural supra-alar seta (DISCOMYZINAE: DISCOMYZINI [in part]) 34

– Thorax without postsutural supra-alar seta or this seta much reduced (no larger than surrounding setulae) 37

34. Wing membrane generally dark with pattern of white maculae (Figs 110, 111) . . . . . .*Actocetor* Becker *sensu lato* 35

– Wing membrane hyaline, or with anterior margin darkened, but not maculate 36

35. Wing with setulae on vein R_{4+5} basad and apicad of crossvein *r–m*; vein M_4 conspicuously sinuous along posterior margin of discal medial cell (*dm*); discal medial cell (*dm*) with at most 1 white macula (Fig. 111) . . . . . *Actocetor* (*Poecilostenia* Bezzi)

– Wing with setulae on vein R_{4+5} only basad of crossvein *r–m*; vein M_4 virtually straight along posterior margin of discal medial cell (*dm*); discal medial cell (*dm*) with 2 or 3 white maculae (Fig. 110) . . . . . .*Actocetor sensu stricto*

36. Head without interfrontal seta; with 2–3 fronto-orbital setae (Fig. 84) . . . . . .*Hostis* Cresson

– Head with interfrontal seta; with 4 fronto-orbital setae (anterior two proclinate, third lateroclinate, fourth lateroreclinate (Fig. 32)) . . . . . *Paratissa* Coquillett

37. Head with pseudopostocellar setae well-developed, length *ca* ½ that of ocellar setae (Fig. 33) . . . . . *Clasiopella* Hendel

– Head with pseudopostocellar setae weakly developed, length considerably < ½ that of ocellar setae (PSILOPINI) 38

38. Antennal base arising from anterodorsal corner of head, at level with dorsal margin of eye (Fig. 82); scape oriented obliquely dorsad, pedicel and postpedicel oriented ventrad, forming acute to right angle with scape (Fig. 82); only proclinate fronto-orbital seta present; antenna greatly elongate, length greater than eye height, postpedicel 3–5 × longer than high (Fig. 82) . . . . . .*Rhynchopsilopa* Hendel

– Antennal base arising lower on head; scape oriented anteriad to obliquely ventrad, pedicel and postpedicel in more or less same ventroclinate plane, forming very obtuse angle with scape; reclinate and proclinate fronto-orbital setae present; antenna normally developed, or only slightly elongate (elongate in some species of *Ceropsilopa* Cresson), length shorter than eye height, length of postpedicel *ca* 2 × its height (*e.g.*, Figs 34, 36, 37, 85) 39

39. Wing vein R_{2+3} running close to costal vein (C) beyond end of vein R_1; discal medial crossvein (*dm–m*) with sharp angle at mid length (Fig. 109) . . . . . .*Clanoneurum* Becker

– Wing vein R_{2+3} well-separated from costal vein (C); discal medial crossvein (*dm–m*) mostly straight or shallowly arched, not angulate 40

40. Antennal pedicel conical, broader apically, without dorsoapical lobe, with weak dorsoapical spine, at most ⅓ length of postpedicel; postpedicel 2–4 × as long as wide (Fig. 34) . . . . . *Ceropsilopa* Cresson

– Antennal pedicel short, subtriangular, with dorsoapical lobe, with strong dorsoapical spine, usually at least ½ as long as postpedicel; postpedicel at most 2 × as long as wide (e.g., Figs 36, 37) 41

41. Antennal arista with at most 3–4 dorsal branches (Fig. 85); head with distance between reclinate and larger proclinate fronto-orbital setae greater than between reclinate seta and inner vertical seta (Fig. 85); setae generally pale (Fig. 85) . . . . . .*Scoliocephalus* Becker

– Antennal arista with at least 5–8 dorsal branches (e.g., Figs 36, 37, 81); head with reclinate and proclinate fronto-orbital setae much closer together than reclinate seta and inner vertical setae (e.g., Figs 36, 37, 81); setae generally dark 42

42. Head with face with transverse striae . . . . . .*Leptopsilopa* Cresson

– Head with face smooth, without transverse striae (e.g., Figs 36, 81) 43

43. Head with 2 facial setae (Fig. 81); antennal pedicel with dorsoapical spine weak, at most ⅓ as long as postpedicel (Fig. 81); thorax with presutural supra-alar seta well-developed, length greater than anterior notopleural seta . . . . . *Diasemocera* Bezzi

– Head with 1 strong facial seta (Fig. 36); antennal pedicel with dorsoapical spine strong, virtually as long as postpedicel (Fig. 36); thorax with presutural supra-alar seta moderately developed, length shorter than anterior notopleural seta . . . . . *Psilopa* Fallén

44. Head with face strongly and coarsely sculptured on at least lower ½; radial sector (*Rs*) bearing 2–4 setulae dorsally . . . . . *Discomyza* Meigen

– Head with face usually smooth; radial sector (*Rs*) without setulae dorsally 45

45. Fore leg strikingly raptorial, with fore femur greatly enlarged and fore tibia with large apical spur (Fig. 116) (GYMNOMYZINAE [in part]: OCHTHERINI) . . . . . *Ochthera* Latreille *sensu lato* 46

– Fore leg normally developed, fore femur slender, fore tibia without large apical spur (as in Fig. 115) 47

46. Head with clypeus narrow, with triangularly pointed apex (Fig. 72); scutellum and mesonotum with stout, spine-like setae (Fig. 72) . . . . . *Ochthera* (*Haplochila* Enderlein)

– Head with clypeus broad, with rounded apex; scutellum and mesonotum with setulae-like setae, not greatly enlarged . . . . . .*Ochthera sensu stricto*

47. Abdominal tergites 3 and 4 enlarged, wider than tergite 2, rugose or pitted; head with face trigonal (Fig. 73) (GYMNOMYZINAE [in part]: GASTROPINI) . . . . . .*Notacanthina* Macquart

– Abdominal tergites 2–4 subequal in width, micro-tomentose, but more or less smooth; head with face normal. 48

48. Head with posterior margin of gena sharply angulate (e.g., Fig. 35); postgena with fine pale setulae; body usually extensively shiny black, although with some grey to whitish micro-tomentum on dorsum; if body brown micro-tomentose, then halter black (GYMNOMYZINAE [in part]: GYMNOMYZINI [in part]) 49

– Head with posterior margin of gena meeting occiput at obtuse angle, broadly rounded; postgena usually with coarse black setulae; body, especially dorsum of thorax, micro-tomentose, usually subshiny, brown to black; halter pale 51

49. Fore femur with stout seta along posteroventral surface, toward apical ⅓; thorax without prescutellar acrostichal setae. . . . . *Athyroglossa* Loew *sensu lato* 50

– Fore femur without stout setae along ventral surface; thorax with prescutellar acrostichal seta . . . . . *Trimerogastra* Hendel

50. Thorax with mesonotal setulae in regular rows; fore femur without posteroventral, spine-like setulae; antennal aristal branches relatively short, length of longest branches *ca* ½ or less height of postpedicel . . . . . *Athyroglossa* (*Parathyroglossa* Hendel)

– Thorax with mesonotal setulae in irregular rows; fore femur bearing 3–7 short, posteroventral, spine-like setulae; antennal aristal branches relatively long, length of longest branches equal to, or greater than, ½ height of postpedicel (Fig. 35) . . . . . *Athyroglossa sensu stricto*

51. Thorax with anterior and posterior notopleural setae inserted equidistant from notopleural suture (as in Fig. 103), if anterior notopleural seta absent, then posterior seta inserted close to suture in posteroventral corner of notopleuron 52

– Thorax with posterior notopleural seta inserted much farther dorsad from notopleural suture than anterior seta (as in Fig. 104) 60

52. Antennal arista long, much longer than postpedicel; head with 1 proclinate fronto-orbital seta; wing rounded at apex of vein R_{4+5}; crossvein *dm–m* usually hyaline (GYMNOMYZINAE [in part]: DISCOCERININI) 53
– Antennal arista short, subequal to length of postpedicel; head with 2–5 proclinate fronto-orbital setae; wing usually pointed at apex of vein R_{4+5}; crossvein *dm–m* usually infuscate (HYDRELLIINAE [in part]: ATISSINI [in part]) 58
53. Thorax with postsutural supra-alar seta strong, distinct, longer than posterior notopleural seta; head with face with dorsoclinate seta at lower lateral extremity (Fig. 38) . . . . . *Diclasiopa* Hendel
– Thorax with postsutural supra-alar seta very short or absent, if distinguishable, then distinctly shorter than posterior notopleural seta; head with face without dorsoclinate seta on lower lateral extremity (e.g., Figs 39–41) 54
54. Hind tibia with preapical, ventral, spur-like seta; head with facial series comprising 2 or 3 large setae, dorsal seta inserted slightly medially from other setae, arising from distinct, shiny papillae, with small, slightly dorsoclinate seta laterad (Fig. 39); body generally micro-tomentose, cinereous species, appearing dull . . . . . *Hecamedoides* Hendel
– Hind tibia without preapical, ventral, spur-like seta; head with facial series comprised of 2 large setae, dorsal seta not arising from shiny papilla, without smaller seta laterad of dorsal seta (e.g., Figs 40, 41); body mostly bare to sparsely micro-tomentose, shiny to subshiny species 55
55. Thorax without notopleuron setulae . . . . . *Ditrichophora* Cresson
– Thorax with notopleuron setulae in addition to 2 large setae (e.g., Fig. 103) 56
56. Head with secondary series of dorsolaterally inclined facial setae laterad to primary series (Fig. 41) . . . . . *Polytrichophora* Cresson
– Head without secondary series of facial setae or suggested only by medially inclined setulae (e.g., Figs 40, 91) 57
57. Head with parafacial wide, with setulae (Fig. 40) . . . . . *Discocerina* Macquart
– Head with parafacial narrow, without setulae (Fig. 91) . . . . . *Orasiopa* Zatwarnicki & Mathis
58. Head without interfrontal setae (Fig. 89); ocellar setae moderately well-developed in ocellar triangle, sometimes just laterad of anterior ocellus (Fig. 89); pseudopostocellar setae greatly reduced, setula-like (Fig. 89) . . . . . *Subpelignus* Papp
– Head with well-developed proclinate interfrontal setae (e.g., Figs 88, 90); ocellar setae reduced in ocellar triangle (e.g., Figs 88, 90); pseudopostocellar setae moderately well-developed, usually slightly divergent (e.g., Figs 88, 90) 59
59. Head with gena high, > ½ eye height (Fig. 90); thorax with acrostichal setulae in 4 rows . . . . . *Cerobothrium* Frey
– Head with gena comparatively low, < ½ eye height (Fig. 88); thorax with acrostichal setulae in 2 rows . . . . . *Schema* Becker
60. Head with ocellar setae inserted anterior to level of anterior ocellus (e.g., Figs 48, 51, 86); wing rounded at apex of vein R_{4+5}; crossvein *dm–m* usually hyaline (GYMNOMYZINAE [in part]: HECAMEDINI) . . . 61
– Head with ocellar seta posterior to level of anterior ocellus (e.g., Figs 54, 55, 88–90) or ocellar setae absent; wing usually pointed at apex of vein R_{4+5}; crossvein *dm–m* usually infuscate (HYDRELLIINAE [in part]: ATISSINI [in part]) 65
61. Head with oral opening large, gaping (Fig. 44); with reclinate fronto-orbital seta only (Figs 43–45); anteroventral margin of face essentially flat, at same level with rest of oral margin; clypeus broad widthwise (Figs 43, 44); thorax without katepisternal seta . . . . . *Elephantinosoma* Becker
– Head with oral opening narrow (e.g., Figs 47, 50); usually with both reclinate and proclinate fronto-orbital seta (e.g., Figs 46–48); anteroventral margin of face emarginated, with narrow clypeus exposed within facial emargination (e.g., Figs 42, 46, 49, 86); thorax usually with katepisternal seta 62
62. Scutellum bearing 3 marginal setae; head with postgenal margin sharp; gena high, > ½ eye height (Figs 42, 46, 47, 49, 50) . . . . . *Hecamede* Haliday *sensu lato* 63
– Scutellum bearing 2 marginal setae; head with postgenal margin rounded; gena short, < ½ eye height (e.g., Fig. 86) 64
63. Head with frontal prominence bare at apex, shiny (Figs 42, 46, 47); proclinate fronto-orbital seta well-developed (Figs 42, 46–48); with interfrontal seta (Figs 42, 46, 47); thorax with acrostichal setae in *ca* 6 irregular rows; katepisternal seta well-developed . . . . . *Hecamede sensu stricto*

– Head with frontal prominence micro-tomentose (Figs 49, 50); proclinate fronto-orbital seta either absent, or weakly developed (Figs 49–51); without interfrontal setae (Figs 49–51); thorax with acrostichal setae in 4 more or less regular rows; without katepisternal seta . . . . . *Hecamede* (*Soikia* Canzoneri & Meneghini)

64. Palpus blackish; face with 2 or more large lateral setae; thorax with 1 well-developed pair of prescutellar acrostichal setae (Fig. 101); 2 katepisternal setae, the second smaller, inserted below larger seta. . . . . *Allotrichoma* Becker

– Palpus mostly yellow; face with 1 large lateral seta (Fig. 86); thorax with prescutellar acrostichal setae greatly reduced or absent; 1 katepisternal seta (poorly developed) . . . . *Eremotrichoma* Giordani Soika

65. Antenna inserted in moderately to very deep sockets (e.g., Figs 52, 53, 87) 66

– Antenna inserted in (at most) rather shallow sockets (e.g., Figs 54, 55, 88–90) 67

66. Fore tibia normal, not bearing large, blunt, black seta at apex; head with antennae somewhat separate, with face between bases wide, with blunt ridge, lacking stout, black setulae (Figs 52, 53); pedicel *ca* as long as height (Fig. 53); arista short, but bearing dorsal branches (Figs 52, 53) . . . . . *Asmeringa* Becker

– Fore tibia bearing large, black, blunt, peg-like seta at apex; head with antennae somewhat approximate, face between antennae with prominent raised triangle bearing numerous stout, black setulae (Fig. 87); pedicel greatly enlarged, height 2 × length; arista reduced to basal, slightly thickened portion (Fig. 87) . . . . . *Isgamera* Giordani Soika

67. Head with face (in lateral view) concave, most prominent at ventral facial margin, lacking dorsally curved setae (Fig. 54). . . . . *Atissa* Haliday

– Head with face (in lateral view) protrudent, prominent just ventrad of antennal bases, bearing large, dorsally curved setae near facial prominence (Fig. 55) . . . . . *Ptilomyia* Coquillett

68. Head with medial facial area and lower facial margin without setae; facial setae inserted in more or less vertical series, parallel with parafacial (e.g., Figs 56–61); subcranial cavity small to large (e.g., Figs 56–61). 69

– Head with medial facial area and lower facial margin setose, latter often with long setae; insertions of facial series of setae convergent above; subcranial cavity large and cavernous (e.g., Figs 62–64, 92–95) 71

69. Thorax without presutural or sutural dorsocentral seta or these inconspicuous (Fig. 102); costal wing vein (C) extending as far as vein R_{4+5}; head as illustrated in Figs 58–61 (DAGINI) . . . . . *Brachydeutera* Loew

– Thorax with presutural or sutural dorsocentral seta, conspicuous; costal wing vein (C) extending as far as vein M_1; head as illustrated in Figs 56, 57 (PARYDRINI) . . . . . *Parydra* Stenhammar *sensu lato* 70

70. Head with face straight to concave in profile (Fig. 57) . . . . . *Parydra* (*Chaetoapnaea* Hendel)

– Head with face convex in profile (Fig. 56) . . . . . *Parydra sensu stricto*

71. Thorax with 3 or 4 postsutural dorsocentral setae (e.g., Fig. 114), anterior 3 sometimes short and weak; disc of proepisternum with few to many fine setulae (e.g., Fig. 114); tarsi with pulvilli greatly reduced or absent; tarsal claws long, gently arched (e.g., Fig. 117) (EPHYDRINI) 72

– Thorax with 2 postsutural dorsocentral setae, both equally strong (e.g., Fig. 92); disc of proepisternum usually bare, sometimes with a few fine setulae; tarsi with pulvilli well-developed; tarsal claws short, distinctly curved (SCATELLINI) 74

72. Antennal postpedicel bearing large lateral seta, just below insertion of arista (Figs 13, 62). . . . . *Setacera* Cresson

– Antennal postpedicel without lateral seta (e.g., Figs 64, 114) 73

73. Head with cruciate interfrontal setae; 3 lateroclinate fronto-orbital setae (Fig. 114) . . . . *Ephydra* Fallén

– Head without cruciate interfrontal setae; 2 lateroclinate fronto-orbital setae (Fig. 64). . . . . *Neoephydra* Mathis

74. Head with 1 lateroclinate fronto-orbital seta (e.g., Fig. 92) 75

– Head with 2–4 lateroclinate fronto-orbital setae (e.g., Figs 63, 93–95) 76

75. Costal wing vein (C) long, extended to apex of vein M_1 (Fig. 113). . . . . *Limnellia* Malloch

– Costal wing vein (C) short, extended to apex of vein R_{4+5} . . . . . *Scatophila* Becker

76. Head with genal seta large, conspicuous (e.g., Figs 93, 94); wing membrane frequently maculate (e.g., Fig. 112) . . . . . *Scatella* Robineau-Desvoidy *sensu lato* 77

– Head with genal seta greatly reduced or absent (e.g., Fig. 63); wing membrane hyaline or slightly infuscate, not maculate 78

77. Thorax with 3 (1 + 2) dorsocentral setae, with anterior seta presutural or sutural (Fig. 93) . . . . . *Scatella* (*Neoscatella* Malloch)

– Thorax with 2 (0 + 2) dorsocentral setae, both postsutural (Fig. 94) . . . . . *Scatella sensu stricto*

78. Thorax with posterior notopleural seta inserted much farther dorsad from notopleural suture than anterior seta (Fig. 104); compound eye longer than high, generally oriented at slightly oblique angle to lower margin of gena (Fig. 63) . . . . . *Haloscatella* Mathis

– Thorax with anterior and posterior notopleural setae inserted equidistant from ventral notopleural suture (as in Fig. 103); compound eye slightly higher than long, appearing round (Fig. 95) . . . . . *Lamproscatella* Hendel

Synopsis of the fauna

Ephydridae include 1,987 valid species that are included in 128 genera (Mathis & Zatwarnicki 1995: 21, plus updates). The Afrotropical fauna currently comprises 69 genera and 379 species and it is estimated here that there are likely to be at least 450 species in the region. Two named fossil species in *Ephydra* and undescribed representatives of the genus *Notacanthina* (as *Beckeriella* Williston) are known (Evenhuis 1994: 449; Zatwarnicki & Hagenlund 2017).

***Achaetorisa* Papp** (Discomyzinae: Risini)**.** A genus of two Old World species occurring in the Afrotropical and Palaearctic Regions. *Achaetorisa salsolae* Mathis & Zatwarnicki, 2017, occurs in the Afrotropics and was described from United Arab Emirates in the Southern Arabian Peninsula (Mathis *et al*. 2017: 646). Papp (1980) described the genus *Achaetorisa* and distinguished it from the genus *Risa*, but did not emphasise the distinctive paired ventral appendages of the female ventral receptacle in *A. brevicornis* Papp, 1980. These appendages appear to be unique to *Achaetorisa*. The biology and immature stages remain unknown. The species can be identified by reference to Mathis *et al*. (2017: 645).

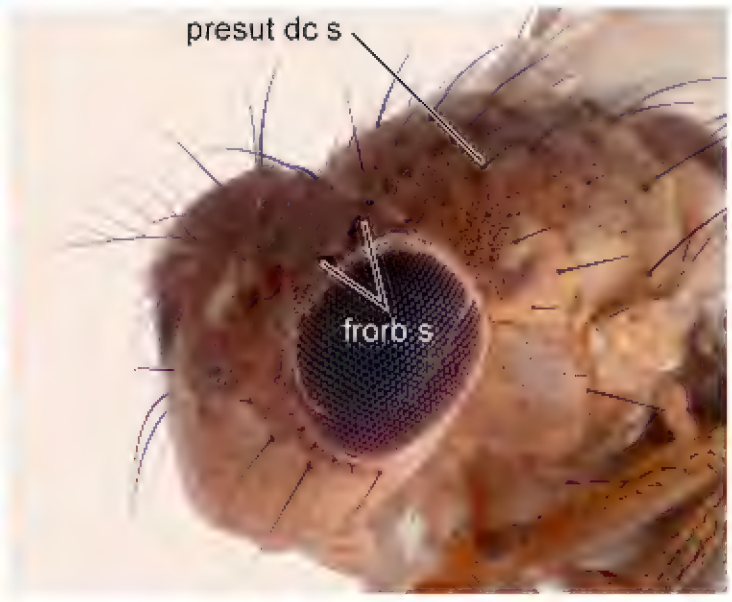
***Actocetor* Becker** (Discomyzinae: Discomyzini)**.** A genus of seven Old World species occurring primarily in the tropical zones of the Afrotropical and Oriental Regions (Dikow & Mathis 2002). Six species in two subgenera, *Actocetor sensu stricto* and *A.* (*Poecilostenia* Bezzi), occur in the Afrotropics. The most widespread species, *A.* (*A.*) *indicus* (Wiedemann, 1824), occurs in the Afrotropical, Oriental and southern Palaearctic Regions and is relatively well-known, due to its distinctive and beautiful colouration, including maculate wings (Figs 110, 111). Not surprisingly, this species has been reported relatively often in the literature. Other species have more limited ranges and occur in East and Southern Africa, Cabo Verde and Madagascar. The literature on other congeners is meagre. Adults are often associated with sandy substrates, especially where there is high organic matter, such as animal dung. Otherwise, virtually nothing is known about their natural history and the immature stages remain unknown. The genus was revised by Dikow & Mathis (2002), who provided an identification key to Afrotropical species.

***Afrolimna* Cogan** (Hydrelliinae: Dryxini)**.** An endemic genus of two described species, *A. carolinika* (Cogan, 1968), from Nigeria and Zimbabwe and *A. keiseri* Cogan, 1968, from Madagascar. *Afrolimna* was first described as a subgenus within *Paralimna* (Cogan 1968, 1980: 662; Mathis & Zatwarnicki 1995: 118), but was accorded generic status following a phylogenetic analysis, which demonstrated a closer relationship with the genera *Corythophora*, *Dryxo* and *Omyxa*, than with *Paralimna* (Mathis & Zatwarnicki 2002). The biology and immature stages remain unknown. The genus was revised by Mathis & Zatwarnicki (2002), who provided an identification key to the two species.

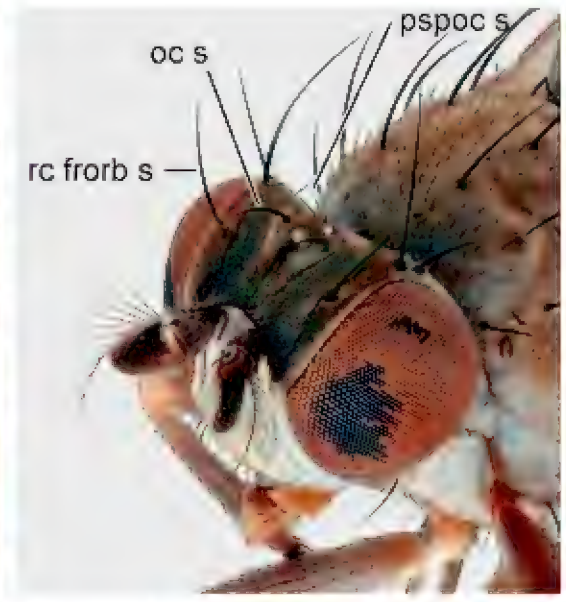
***Allotrichoma* Becker** (Gymnomyzinae: Hecamedini)**.** A genus of 62 described species occurring in all zoogeographical regions, except Antarctica. Sixteen species occur in the Afrotropical Region, all in the nominate subgenus *Allotrichoma sensu stricto*. The genus is mostly associated with freshwater environments. Runyan & Deonier (1979) summarised information on natural history and published the only illustrations of the egg, puparium and cephaloskeleton and photographs of larvae. They further reported that specimens occur in habitats that are rich in decaying organic matter, including limnic wrack, stagnant pools and vertebrate dung (cow, horse, muskrat, pig and raccoon dung). Sand shores and piles of lawn clippings were also added as habitats for adults, which have also been swept from the inflorescences of a wide variety of plant species. Adults have also been collected on decaying fish and crayfish. Larvae are probably scavengers and adults have been reared from dead and decaying arthropods. Currently only males of the subgenus can be identified with certainty. There is currently no identification key to Afrotropical species.

***Asmeringa* Becker** (Hydrelliinae: Atissini)**.** An Old World genus of six described species occurring in the Afrotropical and Palaearctic Regions. All are halophilous and occur in the Afrotropics, with *A. inermis* Becker, 1903 being the most widespread species (Mathis 1984*a*). Although *Asmeringa* is similar through convergence to *Lipochaeta* Coquillett (subfamily Gymnomyzinae, tribe Lipochaetini), the genus is more closely related to *Isgamera*. Deep facial cavities are most pronounced in *Lipochaeta*, but are usually also evident in *Asmeringa*. Perhaps the most interesting structural similarity of this group is the modified antennal arista; frequently this is weakly developed, just a stub, without aristal branches, as in *Lipochaeta* and *Isgamera*. In *Asmeringa*, however, the antenna is short, stub-like, bearing numerous aristal branches that appear to arise near the apex (Figs 52, 53). This last character is unique to *Asmeringa* and not

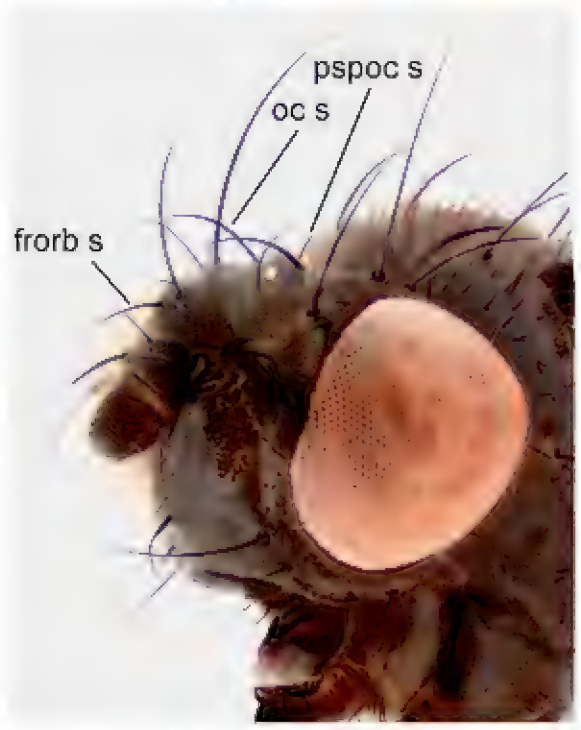
65 *Nostima*



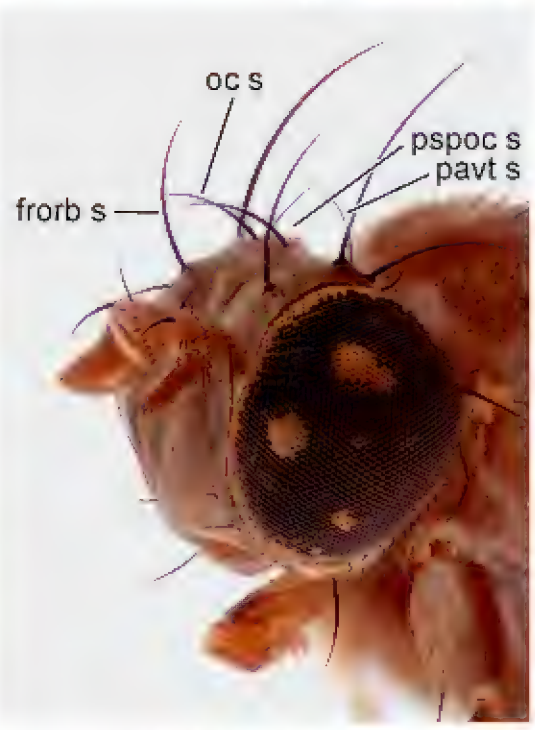
66 *Donaceus*



67 *Notiphila* (*Notiphila*)

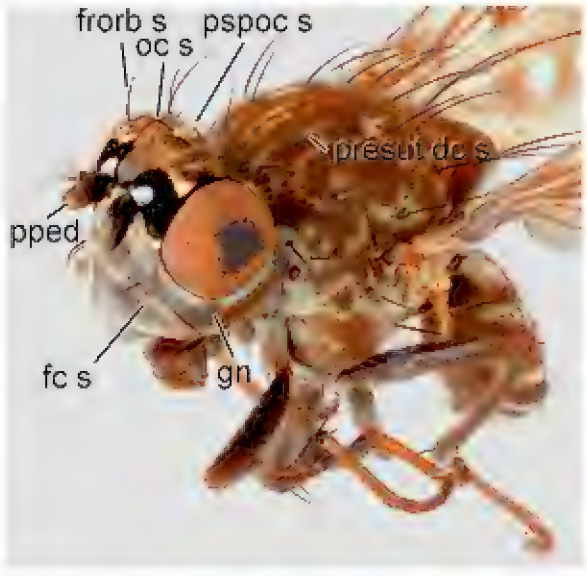


68 *Typopsilopa*

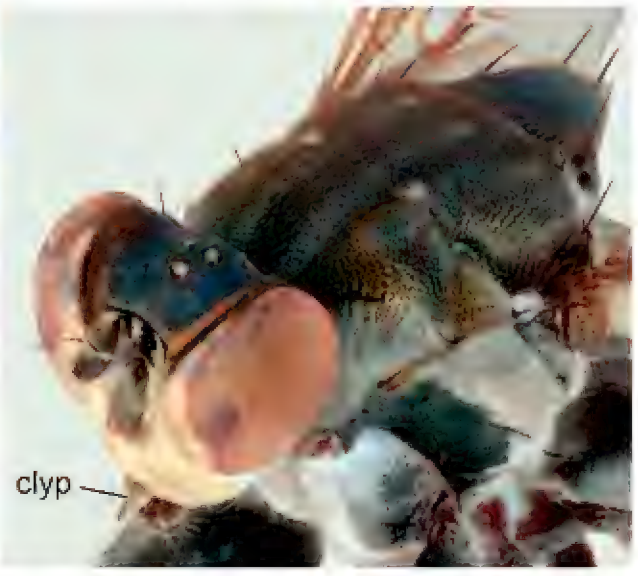


69 *Psilopoidea*

70 *Omyxa*



71 *Paralimna* (*Paralimna*)



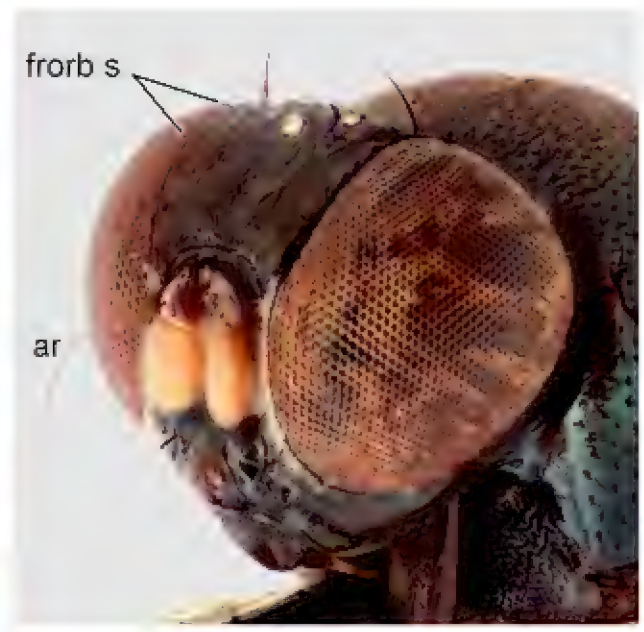
72 *Ochthera* (*Haplochila*)

73 *Notacanthina*

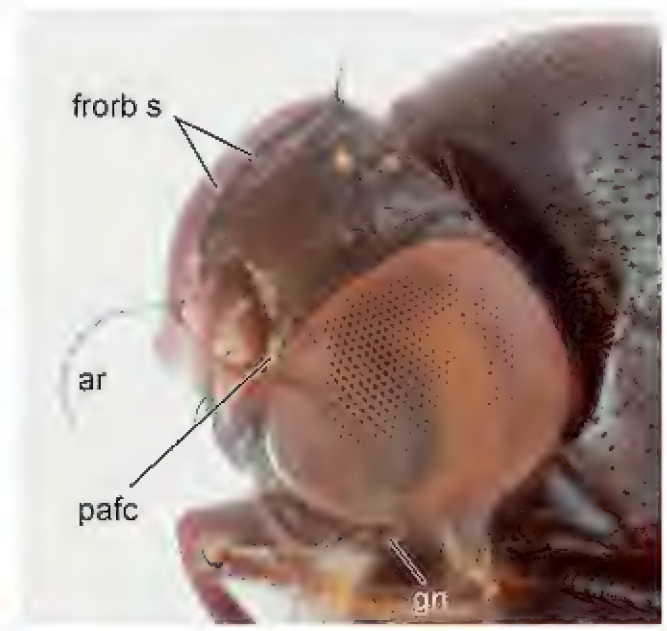
Figs 100.65–73. Heads and thoraces of Ephydridae (anterodorsal views): (65) *Nostima striata* (Lamb); (66) *Donaceus nigronotatus* Cresson; (67) *Notiphila* (*Notiphila*) *fuscofacies* Cogan; (68) *Typopsilopa natalensis* Wirth; (69) *Psilopoidea howardi* Cresson; (70) *Omyxa scuta* Mathis & Zatwarnicki; (71) *Paralimna* (*Paralimna*) *approximata* Cresson; (72) *Ochthera* (*Haplochila*) *insularis* Becker; (73) *Notacanthina fasciata* (Mathis & Grimaldi).

Abbreviations: ar – arista; clyp – clypeus; fc – face; fc s – facial setae; frorb s – fronto-orbital seta(e); gn – gena; oc s – ocellar seta; pavt s – paravertical seta; pped – postpedicel; presut dc s – presutural dorsocentral seta; pspoc s – pseudopostocellar seta; rc frorb s – reclinate fronto-orbital seta.

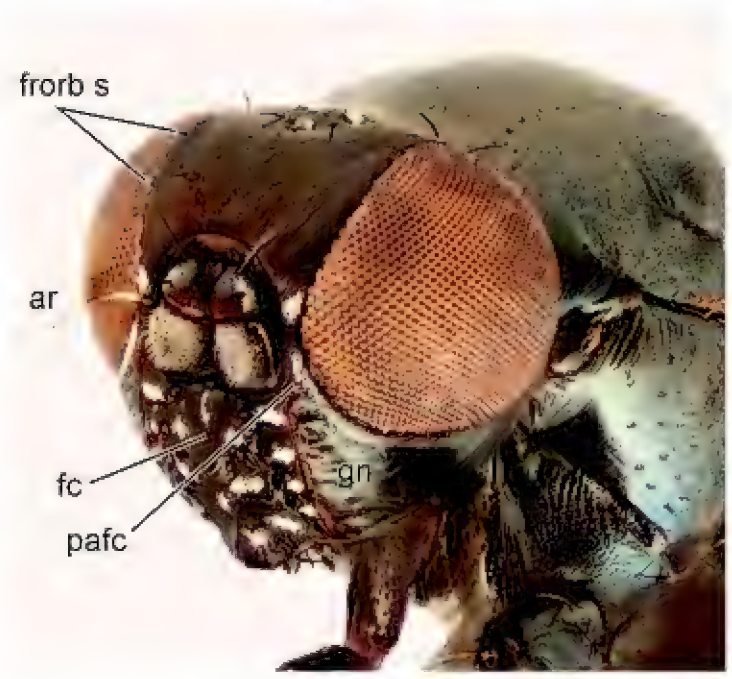
74 *Trimerogastra*



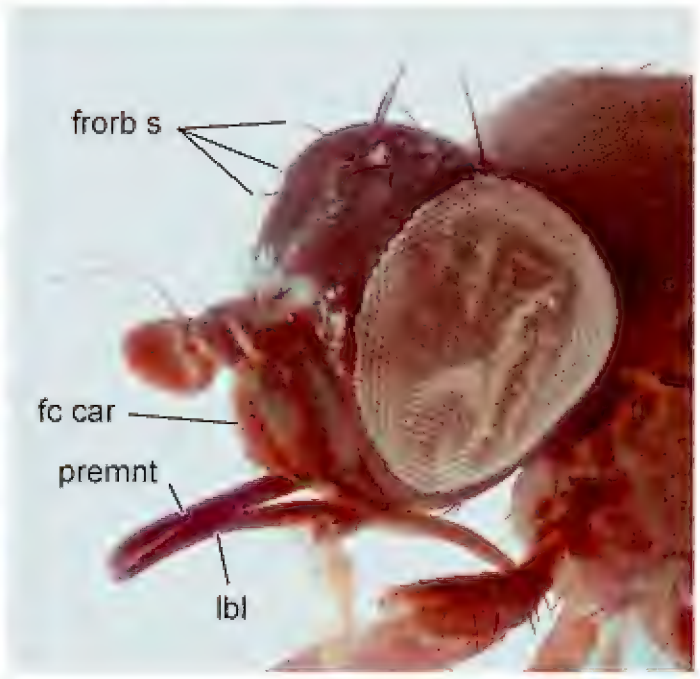
75 *Mosillus*



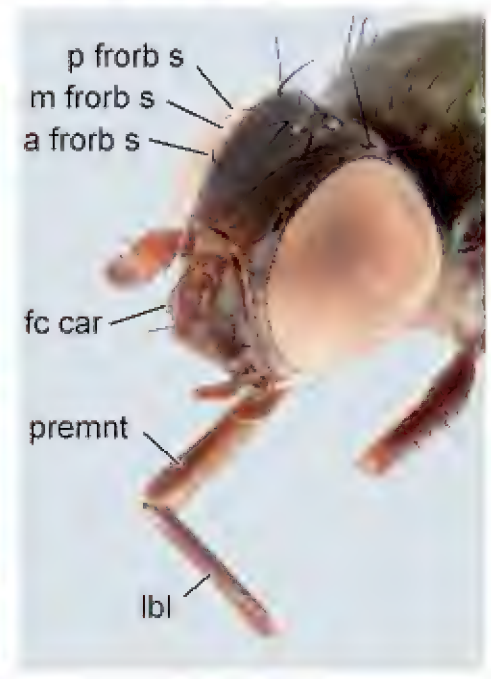
76 *Gymnopiella*



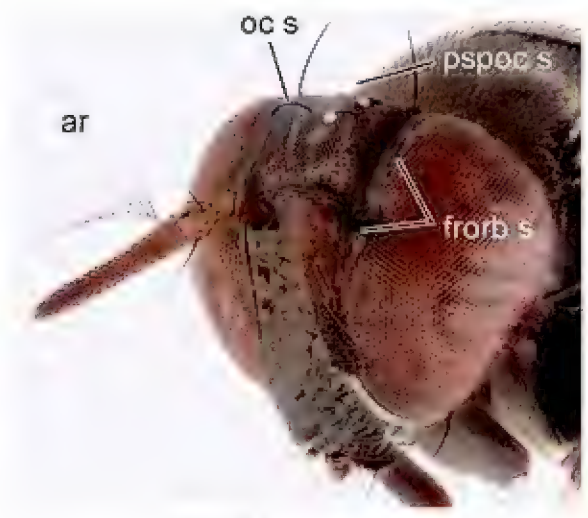
77 *Chlorichaeta*



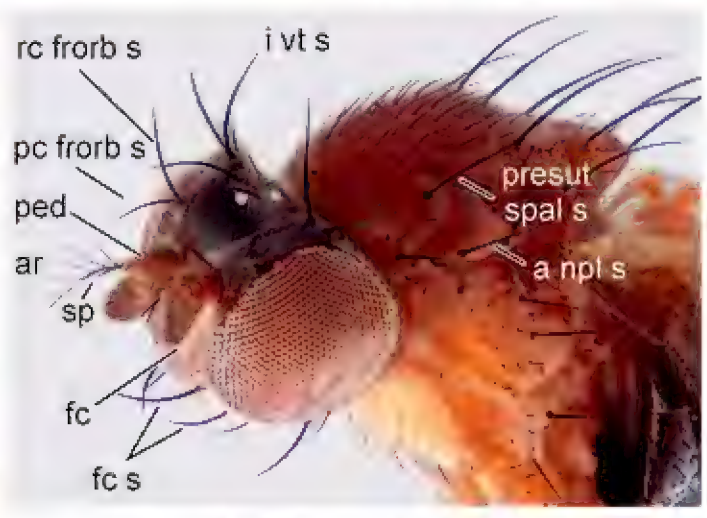
78 *Achetorisa*



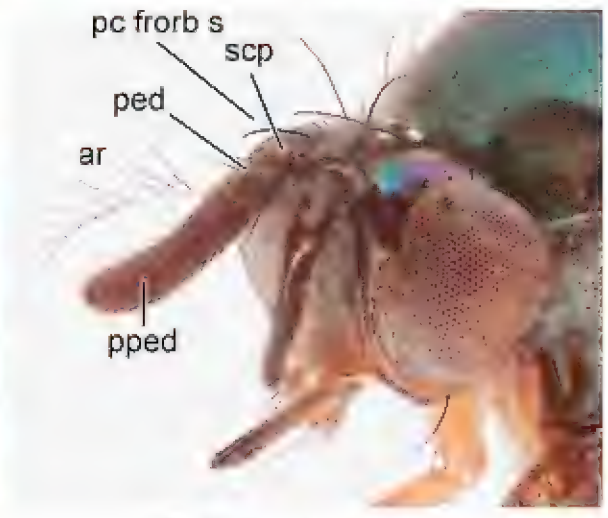
79 *Risa*



80 *Discomyza*



81 *Diasemocera*



82 *Rhynchopsilopa*

Figs 100.74–82. Heads and thoraces of Ephydridae (anterodorsal views): (74) *Trimerogastra cincta* Hendel; (75) *Mosillus beckeri* (Cresson); (76) *Gymnopiella vansomereni* Cresson; (77) *Chlorichaeta africana* Mathis & Zatwarnicki; (78) *Achaetorisa brevicornis* Papp; (79) *Risa longirostris* Becker; (80) *Discomyza dolichocerus* Cresson; (81) *Diasemocera rufithorax* (Becker); (82) *Rhynchopsilopa longicornis* (Okada).

Abbreviations: a frorb s – anterior fronto-orbital seta; a npl s – anterior notopleural seta; ar – arista; fc – face; fc car – facial carina; fc s – facial setae; frorb s – fronto-orbital setae; gn – gena; i vt s – inner vertical seta; lbl – labellum; m frorb s – medial fronto-orbital seta; oc s – ocellar seta; p frorb s – posterior fronto-orbital seta; pafc – parafacial; pc frorb s – proclinate fronto-orbital seta; ped – pedicel; pped – postpedicel; premnt – prementum; presut spal s – presutural supra-alar seta; pspoc s – pseudo-postocellar seta; rc frorb s – reclinate fronto-orbital seta; scp – scape; sp – spine.

only characterises the genus, but also establishes its monophyly. Another character that establishes the monophyly of *Asmeringa* is the shortened basal section of wing vein M_1. Adults are sometimes abundant on shorelines of marine beaches or in inland areas, surrounding saline habitat; otherwise the biology and immature stages remain unknown. The genus was partially revised by Mathis *et al.* (2017), who provided an identification key to species from United Arab Emirates. More southern occurring species can be identified with reference to figures in Mathis (1984*a*) and Kirk-Spriggs *et al.* (2001).

***Athyroglossa* Loew** (Gymnomyzinae: Gymnomyzini)**.** A genus of 37 described species (Fig. 2), occurring in all zoogeographical regions, except the Oriental Region and Antarctica. The genus is divided into two subgenera, the nominate subgenus and *A.* (*Parathyroglossa* Hendel). Ten species occur in the Afrotropics: eight in *Athyroglossa sensu stricto* and *A.* (*P.*) *africana* (Wirth, 1955) and *A.* (*P.*) *hayliensis* Mathis & Zatwarnicki, 2017, in *A.* (*Parathyroglossa*). Larvae of the extralimital species, *A.* (*A.*) *glabra* (Meigen, 1830), are scavengers in decaying vertebrates (Krivosheina & Ozerov 1989). Adults are associated with both lotic and lentic aquatic systems, otherwise the biology and immature stages remain unknown. Although lacking some species, the identification key provided by Canzoneri & Meneghini (1969) is the best available for identification of Afrotropical species.

***Atissa* Haliday** (Hydrelliinae: Atissini)**.** A genus of 15 described species, occurring in all zoogeographical regions, except the Oriental Region and Antarctica. Three species are known from the Afrotropical Region: *A. kairensis* Becker, 1903, from Cabo Verde, Kenya, Sierra Leone and Sudan; the widespread *A. pygmaea* (Haliday, 1833), known from Kenya, Senegal and Sierra Leone in the Afrotropics and *A. vanharteni* Mathis & Zatwarnicki, 2017, described from specimens occurring in the United Arab Emirates. Other species occur in East and West Africa and Cabo Verde. Adult flies are tiny, frequently less than 2 mm in body length, and are found directly on exposed sand or mud with little or no vegetation. As with other genera of the tribe Atissini, *Atissa* occurs almost exclusively where saline aquatic systems occur primarily along maritime coasts, but also inland. Otherwise the biology and immature stages remain unknown. There is no identification key to Afrotropical species.

***Brachydeutera* Loew** (Ephydrinae: Dagini)**.** A genus of 16 described species (Fig. 4) occurring in all zoogeographical regions, except Antarctica. The Afrotropical fauna is relatively diverse, with eight species, including *B. longipes* Hendel, 1913, which was probably introduced from the Oriental Region (Wirth 1964). Other species occur in Central, East and Southern Africa and in Cabo Verde and Madagascar. Although easily recognised, the phylogenetic relationships of the genus are not yet fully resolved and placement in the tribe Dagini remains tentative. Adults and immature stages occur in lentic aquatic habitats, especially small, undisturbed pools and species are seemingly able to tolerate considerable pollution, such as the pooled effluent from coffee processing plants. Keiper & Walton (2000) and Williams (1938) published extensive notes on the biology, including detailed descriptions of the egg, larvae and puparium. Although somewhat out of date, many Afrotropical species can be identified by reference to Wirth (1964).

***Cerobothrium* Frey** (Hydrelliinae: Atissini)**.** An Old World genus of five described species, occurring in the Afrotropical and Palaearctic Regions. Four species occur in the Afrotropics, mostly in insular habitats: Cabo Verde (*C. ptahi* Frey, 1958), Seychelles (*C. insulatum* Mathis & Zatwarnicki, 2003 and *C. ligabuei* (Canzoneri, 1981)) and United Arab Emirates (*C. khorkalba* Mathis & Zatwarnicki, 2017). *Cerobothrium* adults are tiny flies, often less than 1 mm in body length, that occur on coastal sandy shores. Otherwise the biology and immature stages remain unknown. There is no identification key to Afrotropical species.

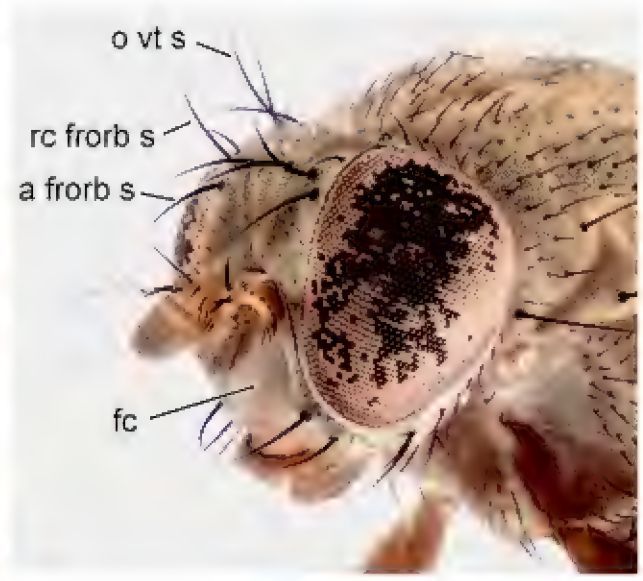
***Ceropsilopa* Cresson** (Discomyzinae: Psilopini)**.** A genus of 23 described species occurring in all zoogeographical regions, except the Palaearctic Region and Antarctica. The Afrotropical fauna is especially rich, with 11 described species that occur widely in the continental Afrotropics, as well as Cabo Verde and the Indian Ocean islands. Adults occur on low-lying vegetation and are sometimes common adjacent to beaches near vegetated sand dunes. Biology and immature stages remain unknown. Canzoneri & Rampini (1998) provided an identification key to Afrotropical species.

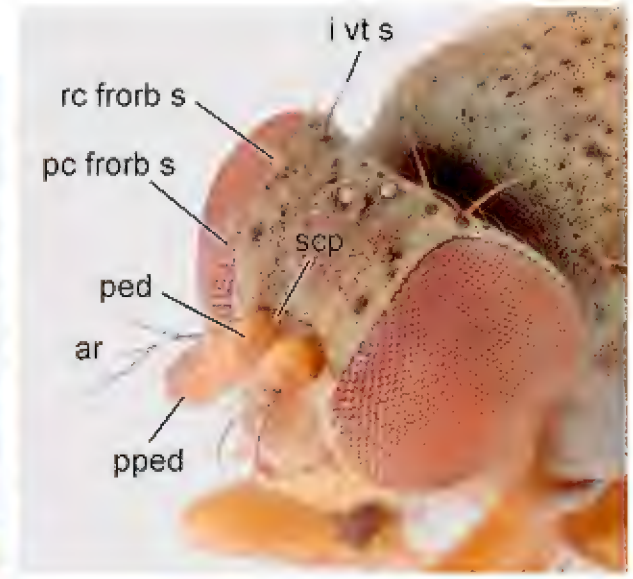
***Chlorichaeta* Becker** (Gymnomyzinae: Gymnomyzini)**.** An Old World genus of seven described species, occurring in the Afrotropical, Australasian/Oceanian, Oriental and Palaearctic Regions. Six species occur widely in Afrotropics (Mathis & Zatwarnicki 1993), including the Indian Ocean islands and Yemen in the Arabian Peninsula. Adults apparently feed as general scavengers in concentrated organic material, such as manure of terrestrial vertebrates. The biology and immature stages are otherwise unknown. *Chlorichaeta* was revised by Mathis & Zatwarnicki (1993), who provided an identification key to Afrotropical species.

***Clanoneurum* Becker** (Discomyzinae: Psilopini)**.** A genus of four described species, occurring in the Afrotropical, Nearctic, Neotropical, Oriental and Palaearctic Regions. The single Afrotropical representative, *C. cimiciforme* (Haliday, 1855), is primarily Palaearctic, but extends into United Arab Emirates in the Southern Arabian Peninsula. Like its congeners, the species appears to have a relationship with plants of the botanical family Chenopodiaceae, particularly the genus *Suaeda*. The biology and immature stages otherwise remain unknown and the genus needs revision.

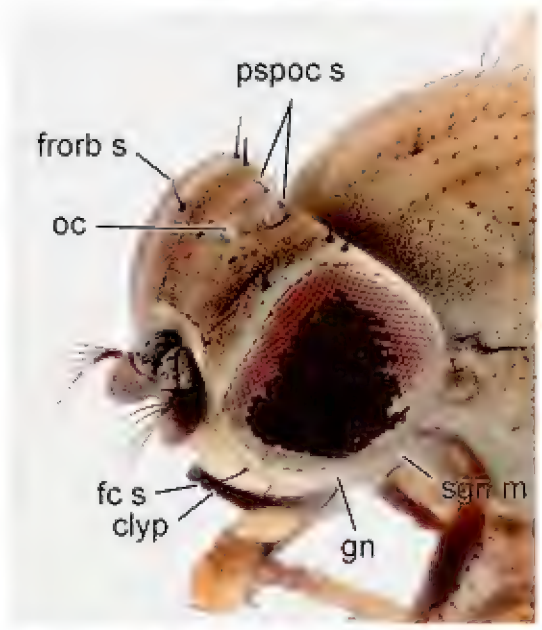
***Clasiopella* Hendel** (Discomyzinae: Discomyzini)**.** A genus of two described species, occurring in the Afrotropical, Australasian/Oceanian, Neotropical and Oriental Regions. The single Afrotropical representative is the widely distributed, *C. uncinata* Hendel, 1914, which probably represents an introduction from the Australasian and/or Oceanian Regions, where the second species occurs (Mathis 1994). Adults occur along maritime coasts and are sometimes common along the margins of mangrove swamps, where there is emergent vegetation. The biology and immature stages otherwise remain unknown. The genus was revised by Mathis (1994), who included an identification key to species.

***Corythophora* Loew** (Hydrelliinae: Dryxini)**.** An endemic genus of two described species. For more than 90 years, *Corythophora* was treated as a junior synonym of *Dryxo* (Bezzi 1908), due to limited access to the name-bearing types of

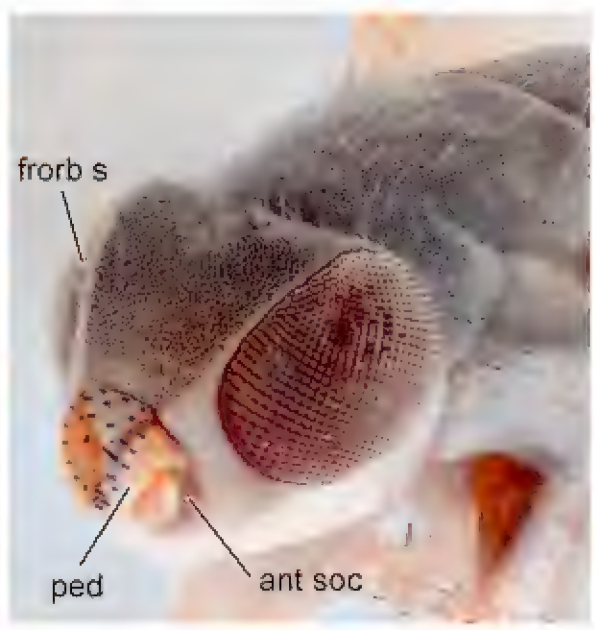




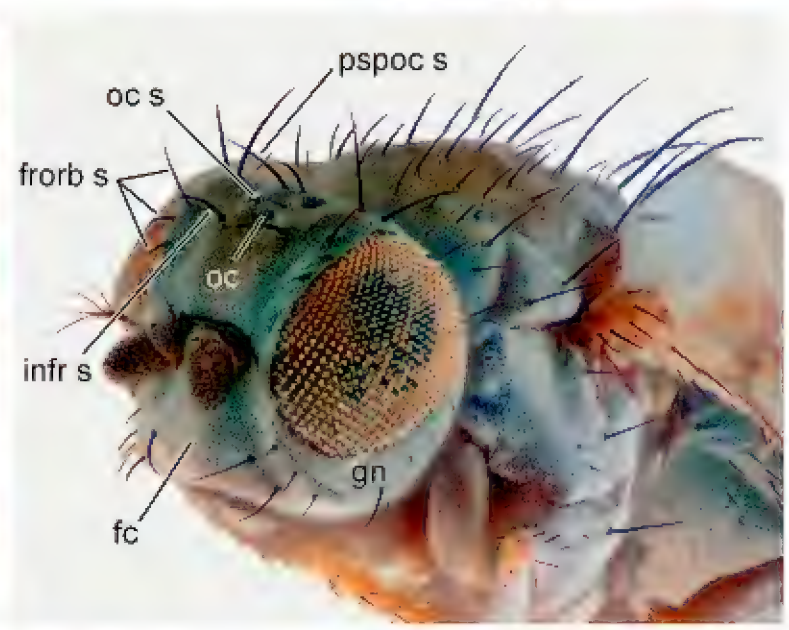
83 *Clanoneurum*



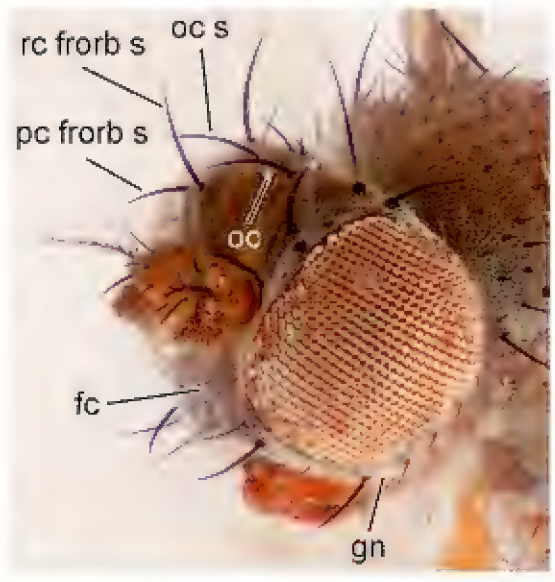
84 *Hostis*



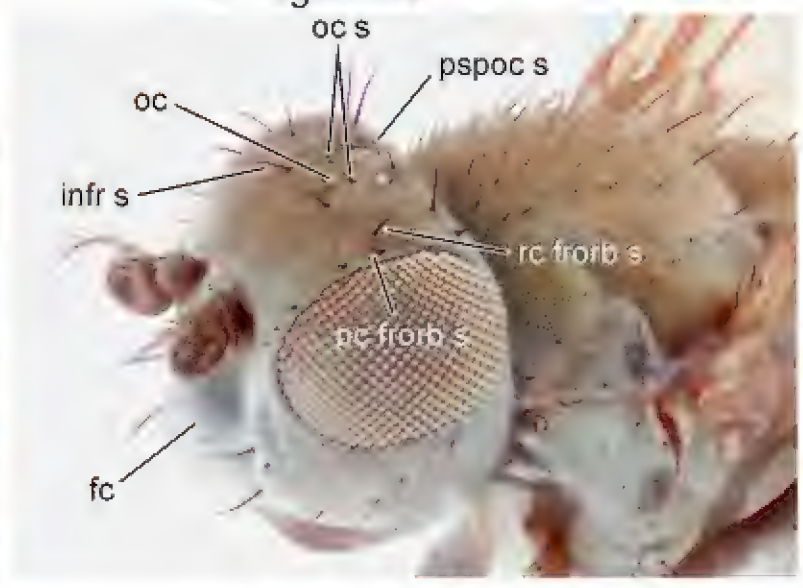
85 *Scoliocephalus*



86 *Eremotrichoma*



87 *Isgamera*



88 *Schema*

89 *Subpelignus*

90 *Cerobothrium*

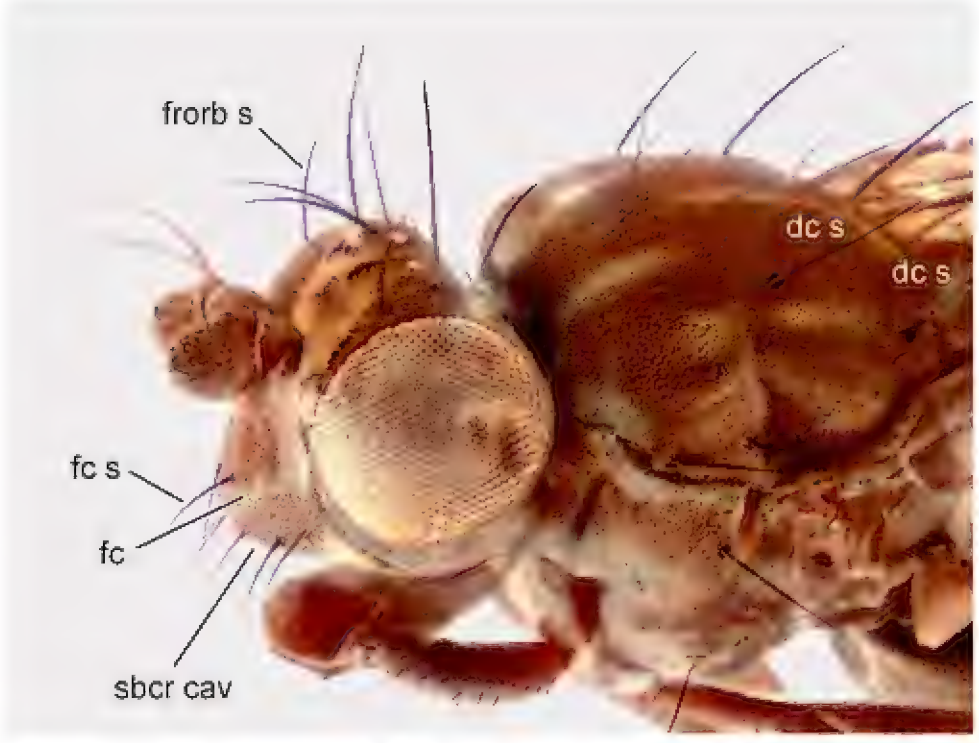
91 *Orasiopa*

Figs 100.83–91. Heads and thoraces of Ephydridae (anterodorsal views): (83) *Clanoneurum cimiciforme* (Haliday); (84) *Hostis guamensis* Cresson; (85) *Scoliocephalus monochaeta* Steyskal; (86) *Eremotrichoma perspiciendum* (Becker); (87) *Isgamera globicornis* Giordani Soika; (88) *Schema aldabricum* Mathis & Zatwarnicki; (89) *Subpelignus maculipennis* Mathis & Zatwarnicki; (90) *Cerobothrium insulatum* Mathis & Zatwarnicki; (91) *Orasiopa mera* (Cresson).

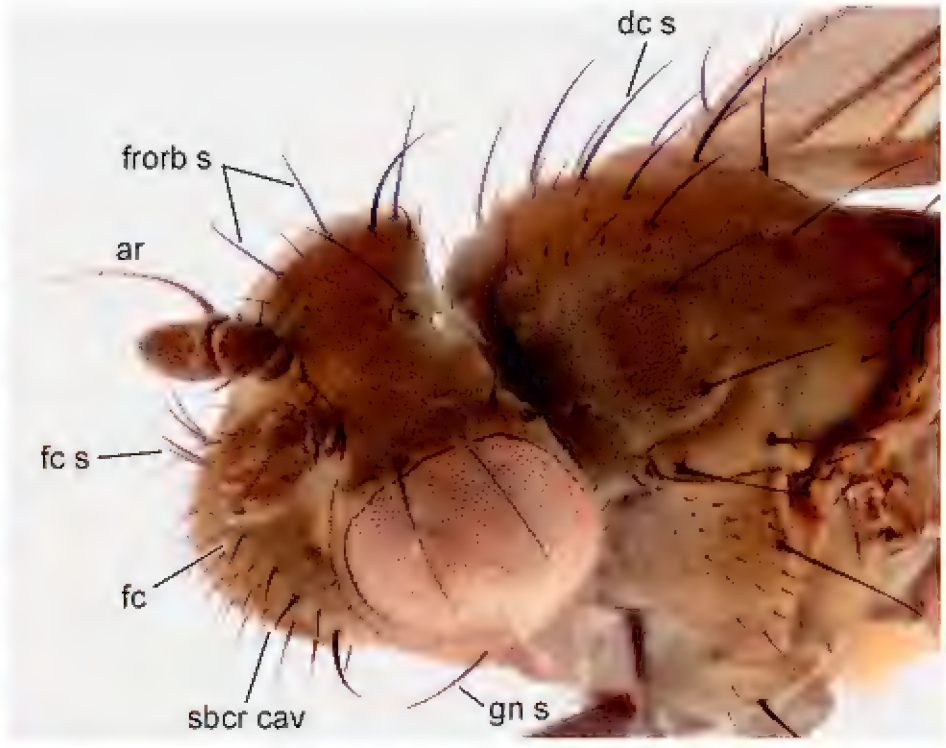
Abbreviations: a frorb s – anterior fronto-orbital seta; ant soc – antennal socket; ar – arista; clyp – clypeus; fc – face; fc s – facial seta(e); frorb s – fronto-orbital seta(e); gn – gena; i vt s – inner vertical seta; infr s – interfrontal seta; o vt s – outer vertical seta; oc – ocellus; oc s – ocellar seta(e); pafc – parafacial; pc frorb s – proclinate fronto-orbital seta; ped – pedicel; pped – postpedicel; pspoc s – pseudopostocellar seta; rc frorb s – reclinate fronto-orbital seta; scp – scape; sgn m – subgenal margin.

Corythophora longipes Loew, 1862. Mathis & Zatwarnicki (2002) studied Loew's type and discovered that *Corythophora* is the senior synonym of *Karema* Cresson, as the type species for both generic names, *C. longipes* and *Karema loewella* Cresson, 1929, are conspecific. Thus, most previous treatments of the species included in *Corythophora*, since Bezzi (1908) were published under the name *Karema* (*i.e.*, Canzoneri & Raffone 1987; Canzoneri & Rampini 1994; Cogan 1968, 1980: 661; Cresson 1929; Mathis & Zatwarnicki 1995: 116 and Wirth 1956, 1960: 393). *Corythophora* was revised by Mathis & Zatwarnicki in 2002 and now comprises two Afrotropical species: *C. flavipes* (Cogan, 1968), described from Madagascar and the widespread Afrotropical species *C. longipes*. Biology and immature stages remain unknown. An identification key to the two species was provided by Mathis & Zatwarnicki (2002).

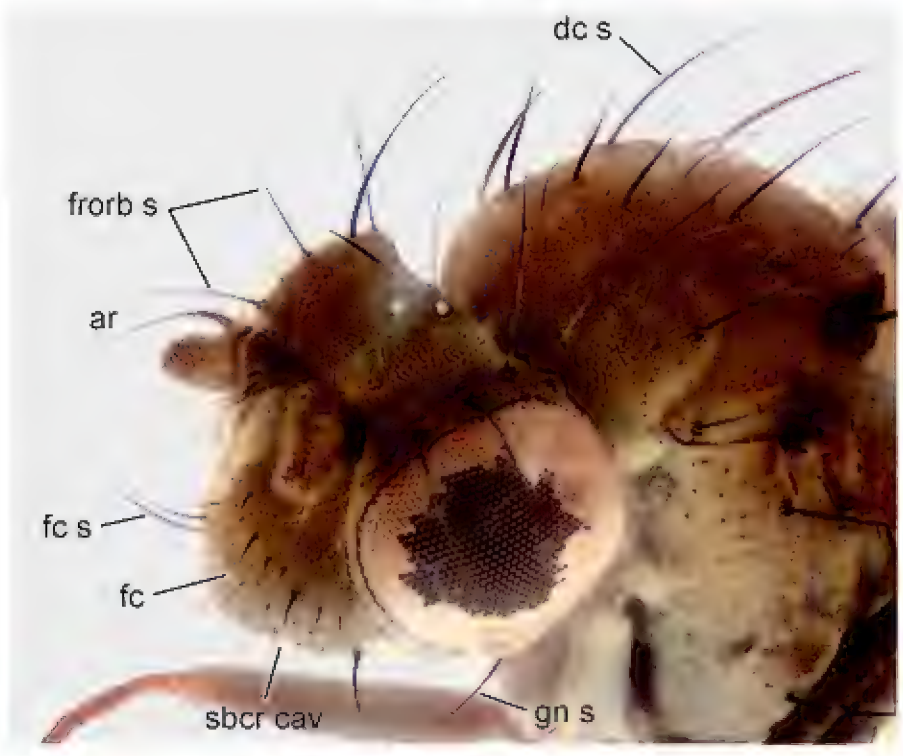
***Diasemocera* Bezzi** (Discomyzinae: Psilopini)**.** A genus of 24 described species, occurring in all zoogeographical regions, except Antarctica. Diversity in the Australasian/Oceanian and Neotropical Regions is scant. Eight species occur in the Afrotropics with greatest diversity on the Southern Arabian Peninsula, especially United Arab Emirates and Yemen. *Diasemocera girschneri* (von Röder, 1889) is probably adventive. Until recently (Zatwarnicki 2018), included species in the genus were regarded as *Psilopa*. *Diasemocera* is included in the tribe Psilopini, close to the non-Afrotropical genus *Trimerina*



92 *Scatophila*



93 *Scatella* (*Neoscatella*)



94 *Scatella* (*Scatella*)

95 *Lamproscatella*

Figs 100.92–95. Heads and thoraces of Ephydridae (anterodorsal views): (92) *Scatophila minima* (Canzoneri & Meneghini); (93) *Scatella* (*Neoscatella*) *stuckenbergi* Wirth; (94) *Scatella* (*Scatella*) *septemfenestrata* Lamb; (95) *Lamproscatella mirabilis* (Canzoneri & Meneghini).

Abbreviations: ar – arista; dc s – dorsocentral seta; fc – face; fc s – facial setae; frorb s – fronto-orbital seta(e); gn s – genal seta; sbcr cav – subcranial cavity.

Macquart and differs from the highly specialised *Psilopa* and related genera, by the number of pseudotracheae (6 or 7), vestiture of the prosternum and characters of the male terminalia. Adults of extralimital species are found on sandy to muddy banks of various aquatic systems that are vegetated. At least one species, *D. leucostoma* (Meigen, 1830), is known as a leaf-miner. Zatwarnicki (2018) recently revised *Diasemocera* and provided an identification key to all known species.

***Diclasiopa* Hendel** (Gymnomyzinae: Discocerinini)**.** A genus of four described species occurring in the Afrotropical, Nearctic and Palaearctic Regions. Three species occur in the Afrotropics: *D. lacteipennis* (Loew, 1862), recorded from Kenya and Sudan and widespread in the Holarctic Realm; *D. nigricornis* Wirth, 1956, described from South Africa; and *D. niveipennis* (Becker, 1896), from Kenya and Sudan and also occurring in the western Palaearctic (Mathis & Zatwarnicki 1995: 16). Adults are mostly associated with largely exposed shores of lentic and lotic aquatic systems; otherwise their biology and immature stages remain unknown. There is currently no identification key to Afrotropical species.

***Discocerina* Macquart** (Gymnomyzinae: Discocerinini)**.** A genus of 20 described species with greatest diversity in the New World. Only the virtually cosmopolitan species, *D. obscurella* (Fallén, 1813), occurs in the Afrotropics and is recorded from Cabo Verde, Democratic Republic of Congo, Kenya and Rodrigues Is. in the Indian Ocean. Adults occur on sandy to muddy banks of various aquatic systems. In the Nearctic Region, Foote & Eastin (1974) described and figured the larva of *D. obscurella* which they reared on a medium of wet peat moss and decaying lettuce and suggested that the larvae were probably utilising micro-organisms. The species can be identified by reference to illustrations provided by Mathis & Zatwarnicki (2010).

***Discomyza* Meigen** (Discomyzinae: Discomyzini)**.** A genus of 10 described species, occurring in all zoogeographical regions, except Antarctica. Six species occur in the Afrotropics that are widely distributed over the continental Afrotropics and in Seychelles in the Indian Ocean. Larvae are malacophagous and develop in a variety of both terrestrial and maritime snails. Zatwarnicki & Cielniak (2015) clarified the status of Afrotropical species in a review of the Afrotropical fauna and provided an identification key to species.

***Ditrichophora* Cresson** (Gymnomyzinae: Discocerinini)**.** A genus of 39 described species, occurring primarily in the Holarctic and Oriental Regions. Two Afrotropical species, *D. metallica* (Canzoneri & Meneghini, 1969) and *D. senegalensis* (Canzoneri, 1981), were described from Democratic Republic of Congo and Senegal respectively, but the generic placement of *D. senegalensis* is uncertain. Adults are associated with lotic aquatic systems, but otherwise nothing is known regarding their biology and immature stages. There is no identification key to Afrotropical species.

***Donaceus* Cresson** (Ilytheinae: Ilytheini)**.** An Old World genus of two described species, occurring in the Afrotropical, Australasian/Oceanian and Oriental Regions. The most widespread congener, *D. nigronotatus* Cresson, 1943, is recorded from Madagascar in the Afrotropics. The genus is distinguished from other genera of Ilytheini in having three (1 + 2) dorsocentral setae. Biology and immature stages remain unknown. The genus was revised by Zack & Sites (1988) and the two species can be identified using the included illustrations.

***Dryxo* Robineau-Desvoidy** (Hydrelliinae: Dryxini)**.** An Old World genus (Fig. 1) of nine described species, occurring in the Afrotropical, Australasian/Oceanian, Oriental and Palaearctic Regions. Four species occur in the Afrotropics: *D. freidbergi* Mathis & Zatwarnicki, 2002, described from Cameroon; *D. margaretae* Cogan, 1968, from Madagascar; *D. ornata* (Macquart, 1844), which is widely distributed in the continental Afrotropics and Yemen in the Arabian Peninsula; and *D. woodi* Cresson, 1936, described from Malawi (Mathis & Zatwarnicki 2002). Species of the genus are among the largest flies in the family, with adult body lengths that sometimes exceed 11 mm. Biology and immature stages remain unknown. An identification key to species was provided by Mathis & Zatwarnicki (2002).

***Elephantinosoma* Becker** (Gymnomyzinae: Hecamedini)**.** An Old World genus of two described species, occurring in the Afrotropical and Palaearctic Regions. *Elephantinosoma chnumi* Becker, 1903, is recorded from Sudan and United Arab Emirates in the Southern Arabian Peninsula and also occurs widely in the Palaearctic Region; and *E. cogani* Mathis & Deeming, 1987, was described from Nigeria. Biology and immature stages remain unknown. Species can be identified by referring to the revision of Mathis & Deeming (1987), but no identification key was provided.

***Ephydra* Fallén** (Ephydrinae: Ephydrini)**.** A genus of 33 described species, occurring in all zoogeographical regions, except Antarctica. Four species occur in the Afrotropics: *E.* (*E.*) *flavipes* (Macquart, 1844) from Chad, Seychelles and Sudan; *E.* (*E.*) *macellaria* Egger, 1862, from Cabo Verde; *E.* (*E.*) *magadiensis* Wirth, 1975, from Kenya; and *E.* (*E.*) *stuckenbergi* Wirth, 1975, from Angola, Botswana, Madagascar, Namibia and South Africa. As with most other genera in the tribe Ephydrini, the larvae have distinct prolegs bearing crochets. Wirth (1975) revised the Old World species and presented an identification key that includes the four Afrotropical species.

***Eremotrichoma* Giordani Soika** (Gymnomyzinae: Hecamedini)**.** An Old World genus of six described species occurring in the Afrotropical and Palaearctic Regions. Two species occur in the Afrotropics: *E. meridionale* (Canzoneri & Vienna, 1989), described from Senegal; and *E. perspiciendum* (Becker, 1903), from Sudan (Mathis 1986*b*). Mathis & Zatwarnicki (2012*a*) reported several synapomorphies that confirm the monophyly of the genus. The species are associated with oases and other aquatic habitats, principally in desert regions. Some of these habitats are saline or alkaline. The biology and immature stages otherwise remain unknown. The genus was revised by Mathis (1986*b*), including an identification key to world species.

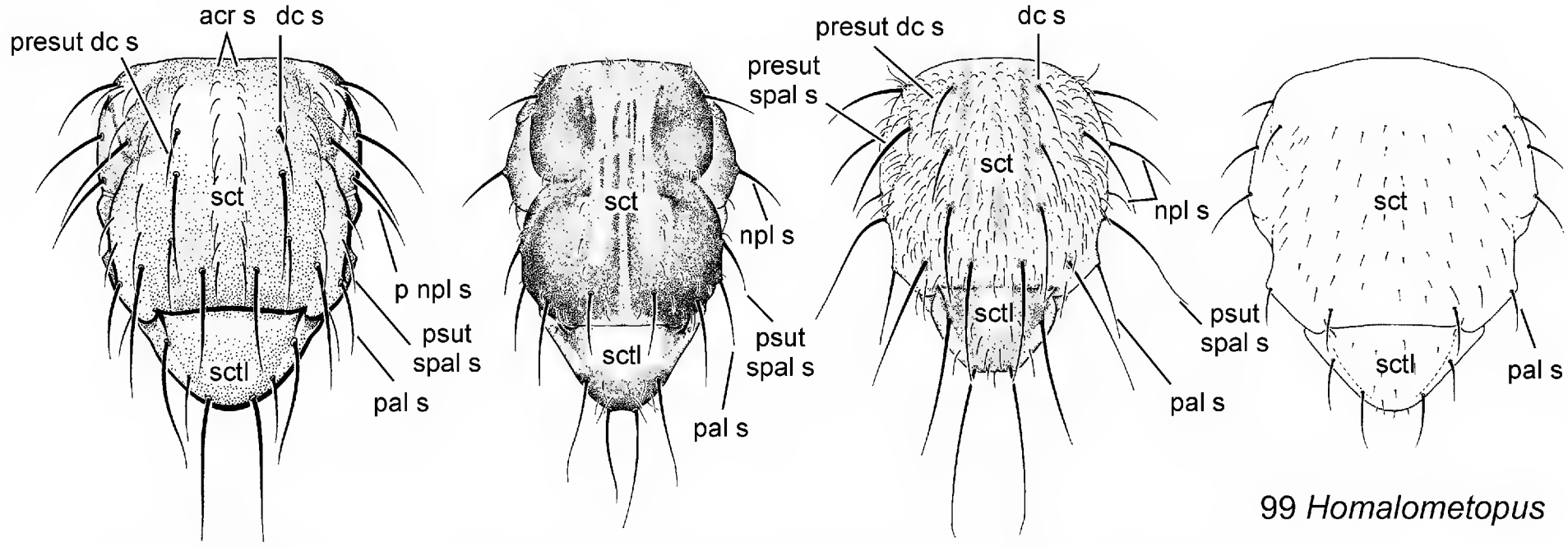
***Glenanthe* Haliday** (Gymnomyzinae: Lipochaetini)**.** A genus of 18 described species occurring in all zoogeographical regions, except the Oriental Region and Antarctica. Two described species occur in the Afrotropics: *G. danielssoni* Zatwarnicki & Mathis, 2012 and *G. namibia* Zatwarnicki & Mathis, 2012 (Zatwarnicki & Mathis 2012). The genus is easily recognised by the pyriform eye (Fig. 29) and only occurs in coastal or inland saline habitats. Biology and immature stages otherwise

remain unknown. Adults of the two Afrotropical species can be identified by reference to Zatwarnicki & Mathis (2012).

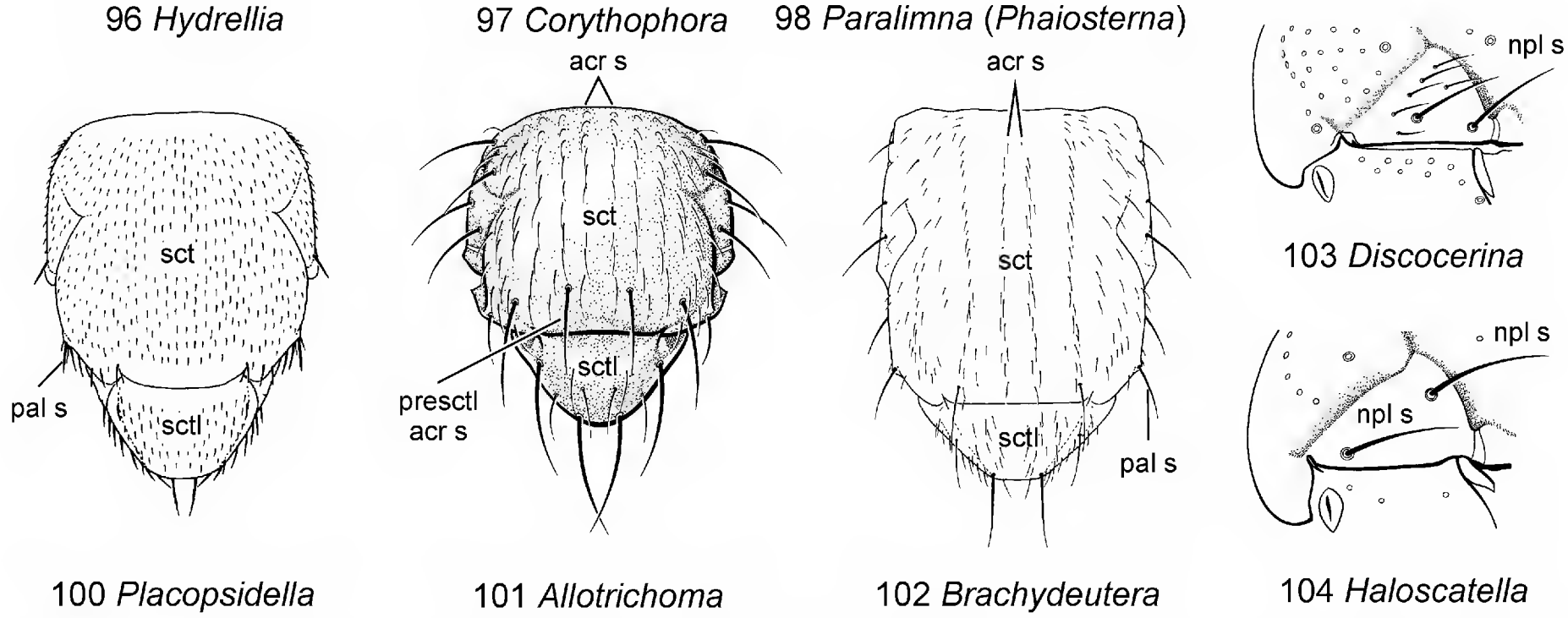
***Gymnopiella* Cresson** (Gymnomyzinae: Gymnomyzini)**.** An Old World genus of two described species occurring in the Afrotropical and Australasian/Oceanian Regions. One species, *G. vansomereni* Cresson, 1946, occurs in the Afrotropics, described from Kenya. Adults are shiny black and uncommon in collections. Biology and immature stages remain unknown.

***Haloscatella* Mathis** (Ephydrinae: Scatellini)**.** A genus of nine described species occurring in the Afrotropical, Nearctic and Palaearctic Regions. A single, primarily Palaearctic, species, *H. dichaeta* (Loew, 1860), is known from South Africa. Dahl (1959) reported this species as being halophilous in habitat preference and that in Sweden it is a distinctly maritime species. Dahl's findings corroborate Collin's (1930) records from the British Isles, where *H. dichaeta* was found to be exclusively coastal in distribution. Foote (2007*b*) recorded larvae of this species (as *Lamproscatella dichaeta*) feeding on decaying seaweed, but the biology and immature stages otherwise remain unknown.

***Hecamede* Haliday** (Gymnomyzinae: Hecamedini)**.** A genus of 12 described species, occurring in all zoogeographical regions, except the Oriental Region and Antarctica (Mathis



96 *Hydrellia* 97 *Corythophora* 98 *Paralimna* (*Phaiosterna*) 99 *Homalometopus*



100 *Placopsidella* 101 *Allotrichoma* 102 *Brachydeutera* 103 *Discocerina* 104 *Haloscatella*

Figs 100.96–104. Thoracic mesonota and notopleura of Ephydridae: (96) mesonotum of *Hydrellia griseola* (Fallén), dorsal view (non-Afrotropical); (97) same, *Corythophora longipes* Loew; (98) same, *Paralimna* (*Phaiosterna*) *decipiens* Loew (non-Afrotropical); (99) same, *Homalometopus albiditinctus* Becker; (100) same, *Placopsidella phaeonotata* Mathis (non-Afrotropical); (101) same, *Allotrichoma simplex* (Loew) (non-Afrotropical); (102) same, *Brachydeutera meridionalis* (Rondani) (non-Afrotropical); (103) notopleuron of *Discocerina obscurella* (Fallén), lateral view (non-Afrotropical); (104) same, *Haloscatella muria* Mathis (non-Afrotropical). Figs 96, 101, 103, 104 (Wirth *et al*. 1987, figs 49, 48, 45, 46, respectively), Figs 97, 98 (Mathis & Zatwarnicki 2002, figs 19, 118), Fig. 99 (Mathis 1984*b*, fig. 6), Fig. 100 (Mathis 1986*a*, fig. 18), Fig. 102 (Mathis & Ghorpadé 1985, fig. 15).

Abbreviations: acr s – acrostichal setae; dc s – dorsocentral setae; npl s – notopleural seta(e); p npl s – posterior notopleural seta; pal s – postalar seta; presctl acr s – prescutellar acrostichal seta; presut dc s – presutural dorsocentral seta; presut spal s – presutural supra-alar seta; psut spal s – postsutural supra-alar seta; sct – scutum; sctl – scutellum.

1993*b*). Eight species, in two subgenera (the nominate subgenus and *H.* (*Soikia* Canzoneri & Meneghini)), occur in the Afrotropics, which is apparently the centre of diversity for the genus. The genus is widely distributed in the continental Afrotropics and occurs on the Indian Ocean islands of Madagascar, Rodrigues Is. and Seychelles and in Oman and Yemen in the Southern Arabian Peninsula. The genus is only associated with maritime coastal habitats, where adults occur on bare sand and/or muddy shores. The immatures are scavengers/saprophytic and may be abundant on dead fish, horseshoe crabs and other marine carrion (Norrbom 1983). Mathis (1993*b*) revised the genus and provided an identification key to Afrotropical species.

***Hecamedoides* Hendel** (Gymnomyzinae: Discocerinini)**.** A primarily Old World genus of 26 described species, occurring in all zoogeographical regions, except Antarctica. The nine Afrotropical species occur widely in the continental Afrotropics and also in Madagascar and Seychelles in the Indian Ocean and in Cabo Verde in the Atlantic Ocean. Numerous Old World species remain to be described and the genus is generally in need of revision. Most species occur in the tropics, although a few extend into temperate regions. Adults are usually found along low-lying shores, especially on mud and sand bars that are often inundated. Frequently the mud and sand have considerable leaf and other organic content, mostly in a state of decay, but elsewhere the sand/mud seemed relatively clean. The immature stages remain unknown, but presumably occur in sand and/or mud, perhaps in the nutrient-rich portions. There is no identification key to Afrotropical species.

***Homalometopus* Becker** (Gymnomyzinae: Lipochaetini)**.** An Old World genus of seven described species, occurring in the Afrotropical and Palaearctic Regions. Two species, *H. albiditinctus* Becker, 1903, recorded from United Arab Emirates and *H. lukinatcha* Mathis, 1984, from Senegal, occur in the Afrotropical Region. The genus is closely related to *Glenanthe* and to the non-Afrotropical genus *Paraglenanthe* Wirth. As in these last-named genera, the antennal arista appears as a brush (more sparsely so in *Homalometopus*), with a ciliate fringe of about equal length above and below (Figs 27, 28). Mathis (1984*b*) and Munari (1988) established the monophyly of *Homalometopus* and its relationships to genera in the tribe Lipochaetini. Biology and immature stages remain unknown. Mathis (1984*b*) revised the genus and included an identification key and illustrations of Afrotropical species.

***Hostis* Cresson** (Discomyzinae: Discomyzini)**.** A monotypic genus, with the single species, *H. guamensis* Cresson, 1945, occurring along maritime shorelines throughout the western Pacific and the Indian Ocean islands of Madagascar and Seychelles. Because of its widespread distribution, there was some scepticism that all specimens were conspecific. Careful examination of external characters and those of the male terminalia, however, indicates a single species. Mathis (1993*a*) postulated that *Hostis* and *Paratissa* are sister taxa and identified 13 morphological synapomorphies that document this relationship. Biology and immature stages remain unknown. The illustrations provided by Mathis (1993*a*) can be used to identify the single included species.

***Hyadina* Haliday** (Ilytheinae: Hyadinini)**.** A genus of 45 described species, occurring in all zoogeographical regions, except Antarctica. Nine species occur in the Afrotropics, distributed in Central, East and West Africa and Cabo Verde. Foote (1993) discovered larvae of the extralimital *H. albovenosa* Coquillett, 1900, on soil-inhabiting colonies of *Anabaena* (Nostocaceae), a genus of filamentous cyanobacteria. The biology and immature stages otherwise remain unknown. There is currently no identification key to Afrotropical species.

***Hydrellia* Robineau-Desvoidy** (Hydrelliinae: Hydrelliini)**.** The largest genus of shore flies, with over 210 described species, occurring in all zoogeographical regions, except Antarctica. The Afrotropical fauna is likewise diverse, with 32 species that are widely distributed in the continental Afrotropics, the Indian Ocean islands of Madagascar and Seychelles and Cabo Verde. Larvae are miners in leaves and stems of various plants, mostly monocotyledons that are associated with aquatic environments. A few species can be serious pests in cereal crops, especially rice (see above). The genus needs revision and no modern identification key to Afrotropical species is currently available.

***Ilythea* Haliday** (Ilytheinae: Ilytheini)**.** A genus of 13 described species, occurring in the Afrotropical, Nearctic, Neotropical and Palaearctic Regions. Although primarily a temperate genus, especially in the Holarctic Realm, the single species, *I. argentata* Canzoneri & Meneghini, 1969, was described from Democratic Republic of Congo. Foote (2007*a*) described the biology of case-bearing larvae of two extralimital species.

***Isgamera* Giordani Soika** (Hydrelliinae: Atissini)**.** An endemic genus of two described species: *I. giordanii* Canzoneri, 1981, recorded from Senegal and Sierra Leone; and *I. globicornis* Giordani Soika, 1956, confined to Madagascar. *Isgamera* was previously placed in the tribe Lipochaetini (Giordani Soika 1956), based on convergent plesiomorphic characters. Based on several synapomorphies, *Isgamera* is better placed in the tribe Atissini, where it is closely related to *Asmeringa*. As with other genera in the Atissini, adults are associated with saline or alkaline aquatic systems. The biology and immature stages remain unknown. Canzoneri (1981) provided a comparison of the two Afrotropical species to facilitate their identification.

***Lamproscatella* Hendel** (Ephydrinae: Scatellini)**.** A genus of 14 mostly northern temperate species, occurring in the Afrotropical, Nearctic, Oriental and Palaearctic Regions (Krivosheina 2004; Mathis 1979*b*). The single Afrotropical representative, *L. mirabilis* (Canzoneri & Meneghini, 1969), was described from Rwanda. Adults are uncommon and occur along the banks of small streams. Biology and immature stages remain unknown. The species can be identified by reference to Mathis *et al.* (2009).

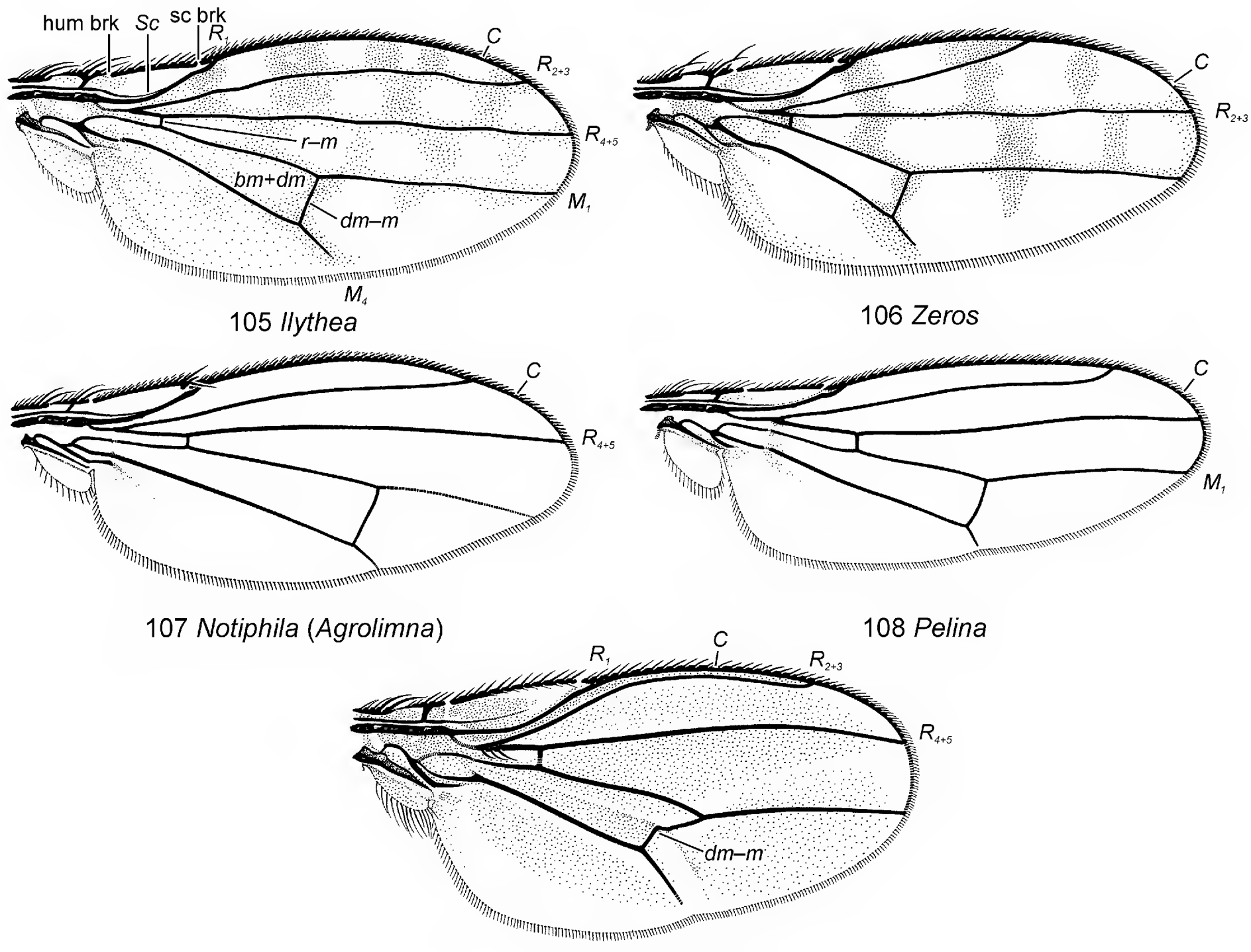
***Leptopsilopa* Cresson** (Discomyzinae: Psilopini)**.** A genus of 15 described species occurring in the Afrotropical, Nearctic, Neotropical and Oriental Regions. The Afrotropical fauna comprises two species: *L. africana* Cresson, 1946, described from Kenya and *L. pollinosa* (Kertész, 1901), described from Singapore (Zatwarnicki *et al.* 2016*a*). Adults can be collected by sweeping vegetation, especially grasses, and some species are common on urban lawns that have not been recently mowed. Mathis & Zatwarnicki (2006) revised the New World species, including the type species and it is not clear whether the Afrotropical and other Old World species are closely

related. Steinly & Runyan (1979) described the biology and larvae of the extralimital species, *L. atrimana* (Loew, 1878). The two Afrotropical species can be identified by reference to Zatwarnicki *et al.* (2016a).

***Limnellia* Malloch** (Ephydrinae: Scatellini)**.** A genus of 22 described species, occurring in all zoogeographical regions, except the Oriental Region and Antarctica. *Limnellia* is primarily a temperate shore fly genus and the only reported Afrotropical species, *L. picta* Canzoneri & Meneghini, 1969, was collected at 1,750 m elevation in Democratic Republic of Congo. Most species have a conspicuously maculate wing (Fig. 113) and a single, lateroclinate fronto-orbital seta. Biology and immature stages remain unknown. The species can be identified by reference to Canzoneri & Meneghini (1969).

***Mosillus* Latreille** (Gymnomyzinae: Gymnomyzini)**.** A genus of seven described species, occurring in the Afrotropical, Nearctic, Neotropical and Palaearctic Regions. Two species occur in the Afrotropics: *M. beckeri* (Cresson, 1925), recorded from Niger, Sudan, Tanzania and Zimbabwe; and *M. bracteatus* Schiner, 1868, described from South Africa. Congeners occur in a variety of habitat types, including the brine resulting from processing coffee beans or brackish-water habitats along the coast. Biology and immature stages remain unknown. The genus was revised by Mathis *et al.* (1993), who provided an identification key to the known species.

***Neoephydra* Mathis** (Ephydrinae: Ephydrini)**.** A genus of 19 almost exclusively Neotropical species, with one Afrotropical species: *N. tristanensis* (Frey, 1954), described from the Atlantic



Figs 100.105–109. Wings of Ephydridae (dorsal views; all non-Afrotropical): (105) *Ilythea spilota* (Curtis); (106) *Zeros flavipes* (Williston); (107) *Notiphila* (*Agrolimna*) *aenigma* Cresson; (108) *Pelina truncatula* Loew; (109) *Clanoneurum americanum* Cresson. Figs 105–109 (Wirth *et al.* 1987, figs 51–53, 57, 50, respectively).

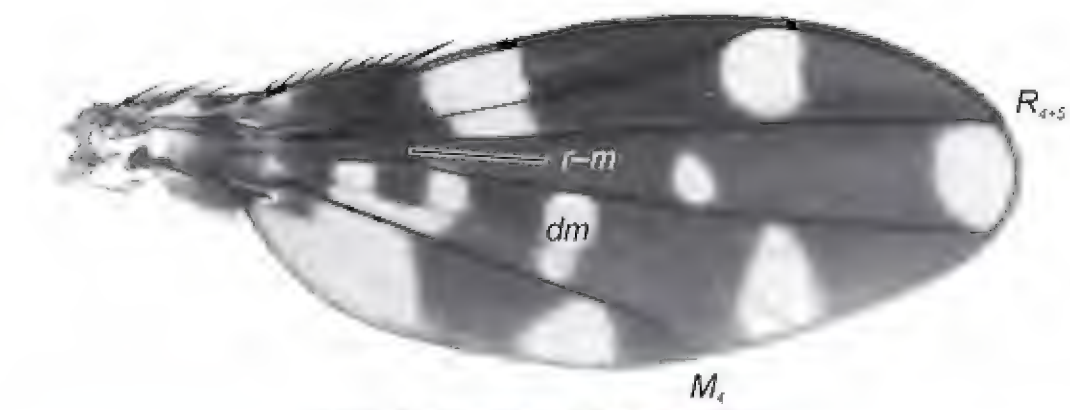
Abbreviations: *bm+dm* – basal medial cell + discal medial cell; *C* – costal vein; *dm–m* – discal medial crossvein; hum brk – humeral break; M_1 – first branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Sc* – subcostal vein; sc brk – subcostal break.

Ocean island of Tristan da Cunha (Mathis & Marinoni 2016). Larvae of *Neoephydra* are typical of the tribe Ephydrini, with eight pairs of claw-bearing prolegs on the ventral surface, the terminal pair being larger and with crochets opposable to those of the other prolegs. The posterior spiracles are borne on a long respiratory tube which bifurcates posteriorly. As with many taxa in the subfamily Ephydrinae, specimens of *Neoephydra* inhabit diverse and somewhat extreme environments. Oliveira (1954) reported on a species with larvae that inhabit warm, algae-covered and often saline water that had accumulated in depressions of large rocks near the seashore. The species can be identified by reference to Mathis & Marinoni (2016).

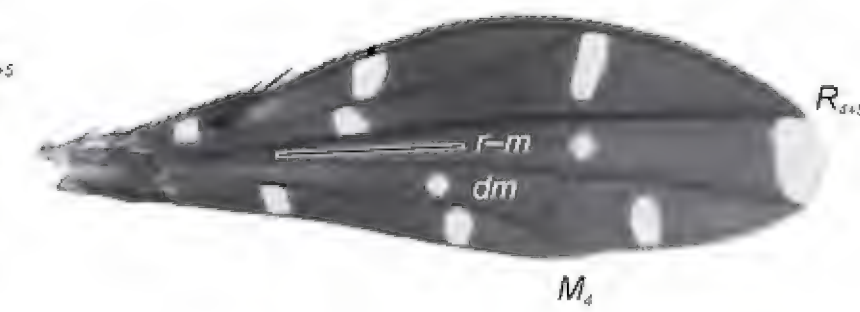
***Nostima* Coquillett** (Ilytheinae: Hyadinini)**.** A genus of 55 described species, occurring in all zoogeographical regions, except Antarctica. There are eight species occurring widely in the continental Afrotropics and also known from Cabo Verde, Seychelles and Oman in the Arabian Peninsula. The Afrotropical fauna is undoubtedly more diverse and needs revision. Foote (1983) discovered larvae of the extralimital species, *N. approximata* Sturtevant & Wheeler, 1954, feeding on the algal genus *Oscillatoria* (Oscillatoriaceae) and certain other related genera of blue-green algae. Biology and immature stages otherwise remain unknown. There is currently no identification key to Afrotropical species.

***Notacanthina* Macquart** (Gymnomyzinae: Gastropini)**.** A genus of 14 described species, occurring in the Afrotropical, Neotropical and Oriental Regions (Zatwarnicki & Hagenlund 2017). Until recently (Evenhuis *et al*. 2016; Zatwarnicki & Hagenlund 2017), species of the genus were usually placed in *Beckeriella*, which in turn had been synonymised with *Gastrops* Williston (Lizarralde de Grosso 1998), but it is here preferred to recognise both genera. These two genera are sister groups (Mathis 1977). *Notacanthina* has a peculiar, disjunct distribution, occurring in the New World tropics, Madagascar (Mathis & Grimaldi 2000: 106) and Philippines in the Oriental Region (Lizarralde de Grosso 1994). Moreover, *Notacanthina* is one of the few shore fly genera for which fossils are known (Dominican amber; Evenhuis 1994: 449). There are records of two species from Madagascar: *N. fasciata* (Mathis & Grimaldi, 2000) and *N. maculata* (Mathis & Grimaldi, 2000), although others undoubtedly remain to be discovered and described, perhaps also from the continental Afrotropics. Biology and immature stages remain unknown, but species of the closely related *Gastrops* are known to be nest parasites of frogs (Leptodactlidae and Hylidae). An identification key to Afrotropical species was provided by Mathis & Grimaldi (2000).

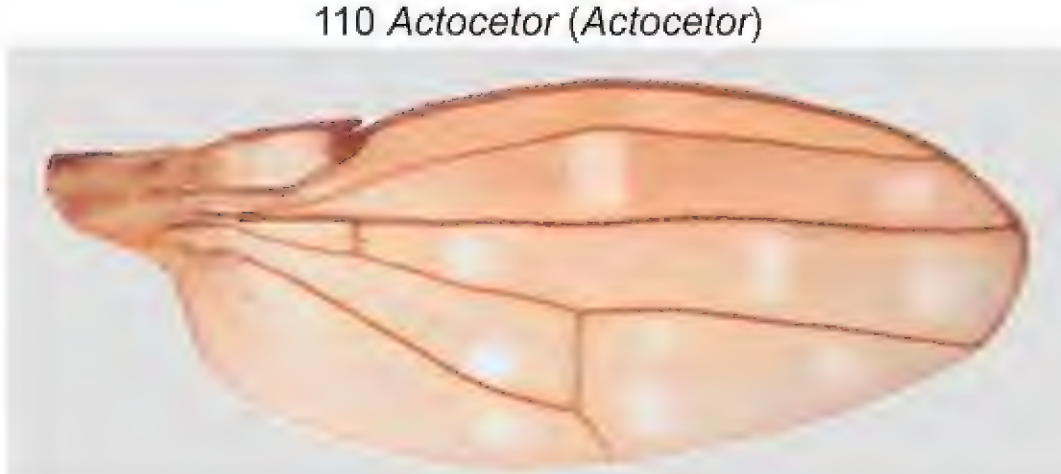
***Notiphila* Fallén** (Hydrelliinae: Notiphilini)**.** A diverse genus of almost 150 described species, occurring in all zoogeographical regions, except Antarctica. There are 25 Afrotropical species that occur widely in the continental Afrotropics, including Yemen in the Southern Arabian Peninsula and several species are endemic to Madagascar. Larvae are detritivores and occur in mud and sand with high organic content, where they obtain oxygen by tapping the rootlets of various aquatic plants with the posterior spiracles (Houlihan 1969). Adults and immature



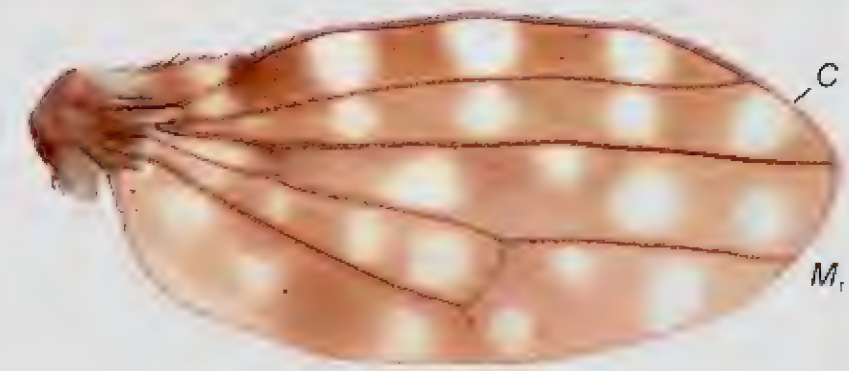
110 *Actocetor* (*Actocetor*)



111 *Actocetor* (*Poecilostenia*)



112 *Scatella* (*Scatella*)



113 *Limnellia*

Figs 100.110–113. Wings of Ephydridae (dorsal views): (110) *Actocetor* (*Actocetor*) *hovus* Giordani Soika; (111) *A.* (*Poecilostenia*) *decemguttatus* (Bezzi); (112) *Scatella* (*Scatella*) *maculosa* Canzoneri & Meneghini; (113) *Limnellia picta* Canzoneri & Meneghini. Figs 110, 111 (Dikow & Mathis 2002, figs 48, 52).

Abbreviations: *C* – costal vein; *dm* – discal medial cell; M_1 – first branch of media; M_4 – fourth branch of media; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein.

stages occur where emergent vegetation, especially monocotyledons, occurs. An identification key to Afrotropical species was provided by Cogan (1968: 286).

***Ochthera* Latreille** (Gymnomyzinae: Ochtherini)**.** A genus of 43 described species, occurring in all zoogeographical regions, except Antarctica. There are 12 Afrotropical species that are widely distributed in the continental Afrotropics and the genus occurs in Cabo Verde, Socotra Is. (Yemen) and Madagascar. The subgenus *O.* (*Haplochila* Enderlein) includes five species, all confined to the Afrotropics and the nominate subgenus includes six Afrotropical species. Adults and larvae are predatory (Simpson 1975) on small terrestrial insects and on midge and mosquito larvae. Simpson (1975) described the immature stages of three Nearctic species. There is currently no identification key to Afrotropical species.

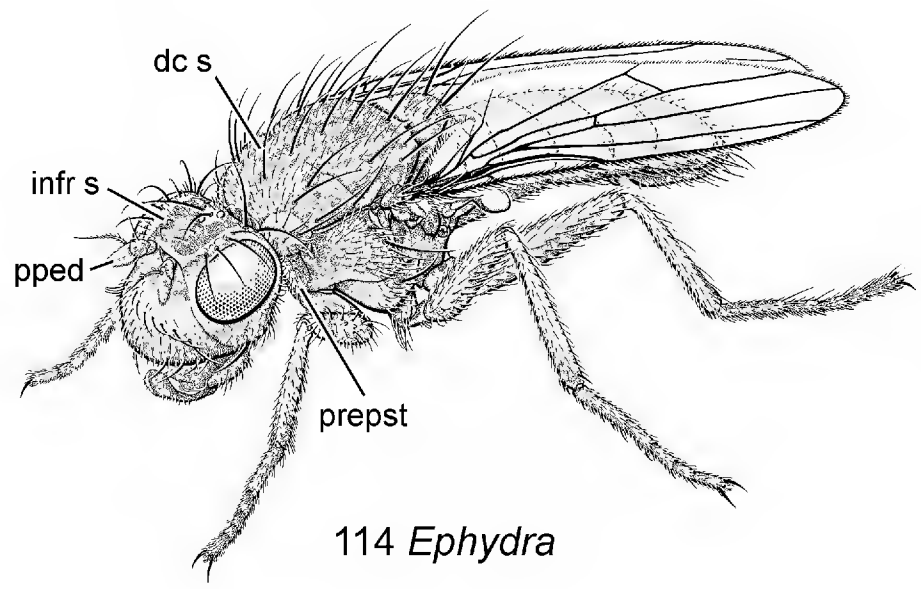
***Oedenopiforma* Cogan** (Hydrelliinae: Dryxini)**.** An Old World genus of five described species, occurring in the Afrotropical, Australasian/Oceanian, Oriental and Palaearctic Regions. Three species occur in the Afrotropics: *O. argentea* (Cogan, 1968), described from Nigeria; *O. madecassa* (Giordani Soika, 1956), recorded from Democratic Republic of Congo and Madagascar; and *O. vockerothi* Mathis & Zatwarnicki, 2012, from United Arab Emirates. Mathis & Zatwarnicki (2002, 2012*b*) identified several synapomorphies that confirm the monophyly of the genus and its close relationship with *Oedenops* and *Papuama* Mathis & Zatwarnicki. Biology and immature stages remain unknown. An identification key to species was provided by Zhang *et al*. (2009), but excludes *O. vockerothi*.

***Oedenops* Becker** (Hydrelliinae: Dryxini)**.** A genus of four described species, occurring in the Afrotropical, Nearctic and Palaearctic Regions. Two species occur in the Afrotropics: *O. afrus* Wirth, 1956, recorded from Kenya and South Africa; and the more widely distributed *O. isis* Becker, 1903, recorded from Cameroon, Ethiopia and Madagascar. Both species occur primarily in subtropical and tropical areas (Mathis & Zatwarnicki 2002). An additional species, *O. nudus* (Coquillett, 1902), occurs in the New World. Adults are found mostly on bare sandy to muddy margins of rivers and streams and occasionally along maritime beaches, the biology and immature stages otherwise remain unknown. An identification key to Afrotropical species was provided by Mathis & Zatwarnicki (2002).

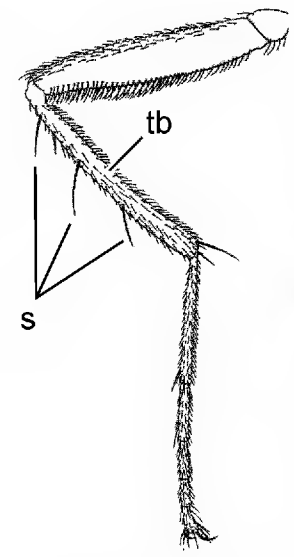
***Omyxa* Mathis & Zatwarnicki** (Hydrelliinae: Dryxini)**.** A monotypic genus, with the single described species, *O. scuta* Mathis & Zatwarnicki, 2002, recorded from Oman in the Afrotropical part of the Arabian Peninsula and from the Oriental Region. The genus is related to *Corythophora* and *Dryxo* in the tribe Dryxini and adults are characterised (in part) by reduced setation (Fig. 70). Little else is known regarding the genus and the biology and immature stages remain unknown.

***Orasiopa* Zatwarnicki & Mathis** (Gymnomyzinae: Discocerinini)**.** An Old World genus of 15 described species, occurring in the Afrotropical, Australasian/Oceanian, Oriental and Palaearctic Regions. Three species occur in Seychelles (including Aldabra), namely: *O. apiculata* Mathis & Zatwarnicki, 2003, *O. mathisi* Zatwarnicki, 2002 and *O. mera* (Cresson, 1939). One species, *O. opa* Zatwarnicki, 2002, is known from United Arab Emirates and *O. mera* is likely to be found more widely as an adventive species in the continental Afrotropics. Adults are associated with coastal marine habitats, especially the wrack zone. The biology and immature stages otherwise remain unknown. The genus was revised by Zatwarnicki (2002), who provided an identification key to species, but this does not include *O. apiculata*.

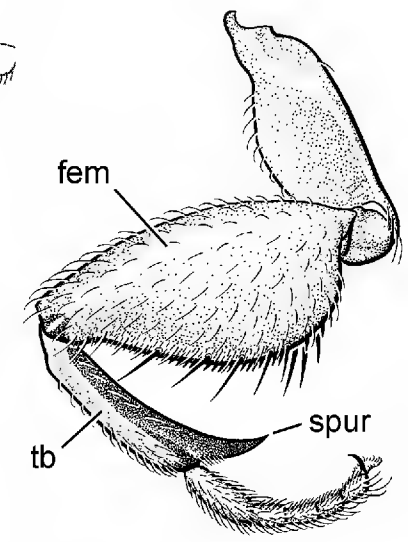
***Paralimna* Loew** (Hydrelliinae: Dryxini)**.** A large shore fly genus, with over 95 described species, occurring in all zoogeographical regions, except Antarctica. Forty-one species are



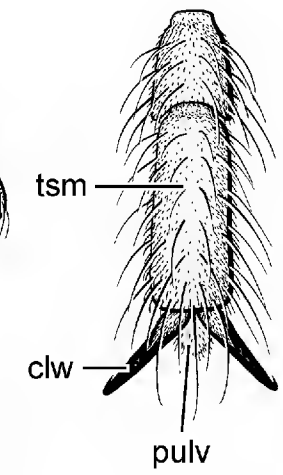
114 *Ephydra*



115 *Notiphila* (*Notiphila*)



116 *Ochthera* (*Ochthera*)



117 *Ephydra*

Figs 100.114–117. Habitus and leg characters of Ephydridae (all non-Afrotropical): (114) habitus of *Ephydra riparia* Fallén, oblique view; (115) mid leg of *Notiphila* (*Notiphila*) *scalaris* Loew, lateral view; (116) left fore leg of *Ochthera* (*Ochthera*) *mantis* (De Geer), posterior view; (117) terminal segments of fore tarsus of *E. subopaca* Loew, dorsal view. Figs 114, 116, 117 (Wirth *et al*. 1987, figs 1, 63, 60, respectively), Fig. 115 (Mathis 1979*a*, fig. 5).

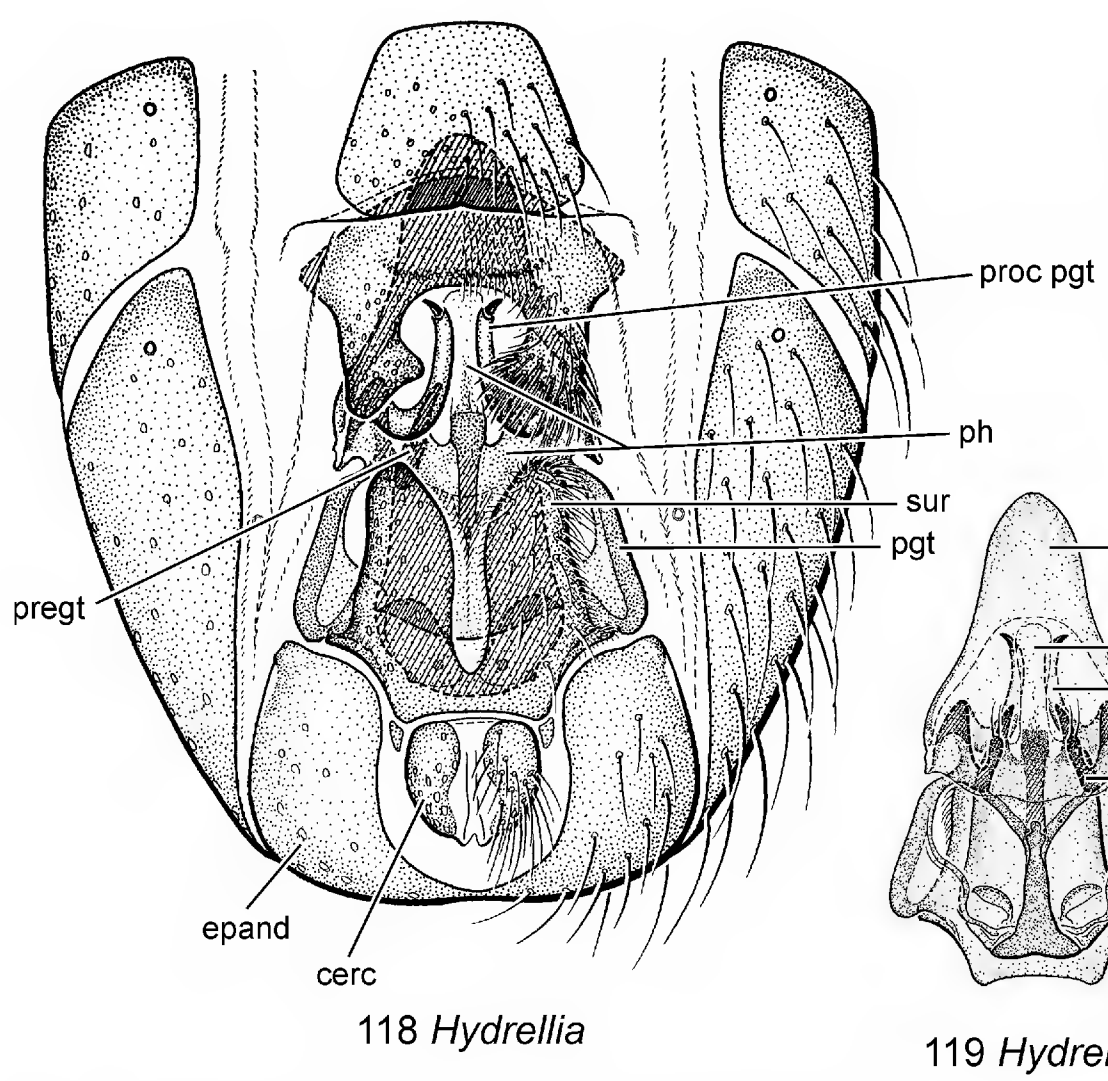
Abbreviations: clw – claw; dc s – dorsocentral seta; fem – femur; infr s – interfrontal seta; pped – postpedicel; prepst – proepisternum; pulv – pulvillus; s – setae; spur – spur; tb – tibia; tsm – tarsomere.

widely distributed in the continental Afrotropics, as well as in Cabo Verde, the Indian Ocean islands of Madagascar and Seychelles and in Yemen in the Southern Arabian Peninsula. *Paralimna*, which are relatively large for shore flies (body length: 2.0–8.7 mm), occur on the muddy and/or sandy shorelines of various aquatic systems. Scheiring & Connell (1988) noted that *Paralimna* larvae feed on plant detritus in the wet mud of pond margins, but otherwise little is known of their biology. Cogan's (1968) revision of the subgenus *Paralimna sensu stricto* is useful for identifying Afrotropical species and species of the subgenus *P.* (*Phaiosterna* Cresson), which were more recently revised, can be identified using Mathis & Zatwarnicki (2002).

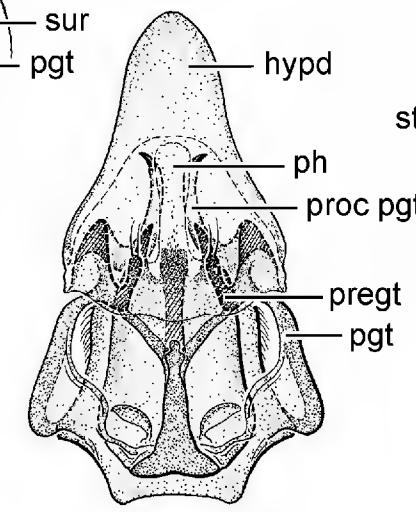
***Paratissa* Coquillett** (Discomyzinae: Discomyzini)**.** A genus of four described species occurring in the Afrotropical, Australasian/Oceanian, Nearctic and Neotropical Regions. A single species, *P. coriacea* (Lamb, 1912), occurs in the Afrotropics, on the Indian Ocean islands of Madagascar and Seychelles. Species of the genus are very similar externally and thus far *P. coriacea* is the only congener that can be distinguished without examination of the male terminalia. The legs are dark coloured, usually blackish brown to black and are concolourous with the pleural area. Structures of the male terminalia also distinguish it, especially the shape of the surstylus, which is similar in shape to that of *Hostis guamensis*, being roughly rectangular in posterior view, but with the lateral margin rounded and the medial margin slightly concave and the postgonite has a single long process. The immature stages presumably occur in wrack and specimens are sometimes abundant where large windrows of wrack have accumulated in protected embayments; the biology and immature stages otherwise remain unknown. The species can be identified by reference to Mathis (1993*a*).

***Parydra* Stenhammar** (Ephydrinae: Parydrini)**.** A primarily north temperate genus of almost 75 described species (Fig. 3), occurring in all zoogeographical regions, except Antarctica. There are five Afrotropical species that are widely distributed in the continental Afrotropics and also occur on Saint Helena Is. and in Seychelles. The immature stages occur in muddy to sandy substrates associated with aquatic environments; a couple of extralimital species are known as larvae, but otherwise, little is known about their biology. There is currently no identification key to Afrotropical species.

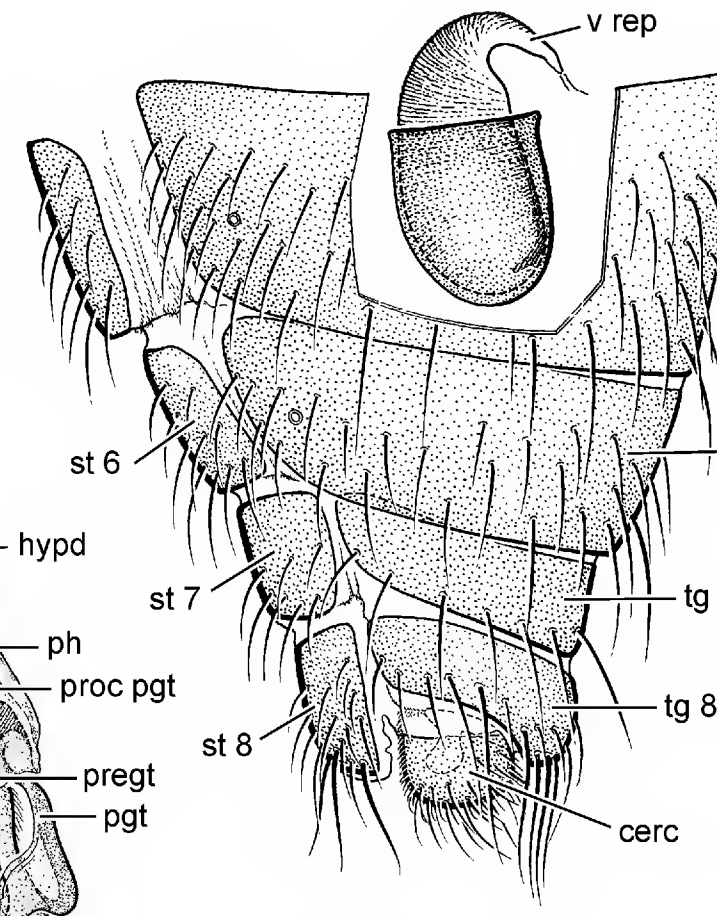
***Pelina* Haliday** (Ilytheinae: Hyadinini)**.** A primarily Holarctic genus of 22 described species, occurring in the Afrotropical, Nearctic, Neotropical and Palaearctic Regions. Only two Central African species occur in the Afrotropics: *P. abdominalis* Canzoneri & Meneghini, 1969, described from Rwanda and *P. cupreofasciata* Giordani Soika, 1956, recorded from Democratic Republic of Congo and Rwanda. Among genera of the tribe Hyadinini, *Pelina* is distinguished in having both the costal wing vein (*C*) and vein R_{2+3} elongated and in possession of both outer and inner vertical setae (Fig. 108). Foote (1981*b*)



118 *Hydrellia*



119 *Hydrellia*



120 *Paralimna* (*Paralimna*)

Figs 100.118–120. Male and female terminalia of Ephydridae (all non-Afrotropical): (118) male terminalia of *Hydrellia griseola* (Fallén), ventral view; (119) same, internal structures; (120) female terminalia of *Paralimna* (*Paralimna*) *punctipennis* (Wiedemann), lateral view. Figs 118–120 (Wirth *et al*. 1987, figs 66, 67)

Abbreviations: cerc – cercus; epand – epandrium; hypd – hypandrium; pgt – postgonite; ph – phallus; pregt – pregonite; proc pgt – process of postgonite; st – sternite; sur – surstylus; tg – tergite; v rep – ventral receptacle.

described the biology and immature stages of the extralimital species *P. truncatula* Loew, 1878. Canzoneri & Meneghini (1969) provided an identification key to Afrotropical species.

***Philygria* Stenhammar** (Ilytheinae: Hyadinini)**.** A genus of 37 described species, occurring in all zoogeographical regions, except the Australasian/Oceanian Region and Antarctica. Six Afrotropical species are recorded from East, Central and Southern Africa. Adults occur more commonly in somewhat dry, grassy habitats that are not immediately associated with aquatic habitats. Larvae of *Philygria* are closely associated with habitats where blue-green algae are growing on the soils' surface and are algae-feeders. Hollmann-Schirrmacher (1998) published a world revision, but this should be used with caution, as the illustrations are misleading.

***Placopsidella* Kertész** (Gymnomyzinae: Gymnomyzini)**.** A genus of eight described species, occurring in all zoogeographical regions, except Antarctica. Three species occur in the Afrotropics: *P. cynocephala* Kertész, 1901, from Seychelles; *P. grandis* (Cresson, 1925), recorded from Sierra Leone; and *P. signatella* Enderlein, 1912, from Madagascar and Seychelles. All three may be adventive to the region (Mathis 1986*a*). Kirk-Spriggs (1986) and Tenorio (1980: 350) reported on the biology of *P. cynocephala* and the extralimital species *P. marquesana* (Malloch, 1933), respectively. Larvae of both species apparently feed as scavengers on dead marine invertebrates that have become stranded on the beach. Adults often occur on seaweed and other debris on maritime beaches. The three Afrotropical species can be identified by reference to Mathis (1986*a*).

***Polytrichophora* Cresson** (Gymnomyzinae: Discocerinini)**.** A genus of 32 described species, occurring in all zoogeographical regions, except Antarctica (Mathis & Zatwarnicki 2012*c*). The genus is divided into two subgenera, the nominate subgenus, plus *P.* (*Sklodowskopa* Zatwarnicki). The Afrotropical fauna comprises eight widely distributed species (including one in Seychelles), all in the subgenus *P.* (*Sklodowskopa*), which is undoubtedly more diverse in the region. *Polytrichophora* belongs to the *Discocerina*-group of genera (Zatwarnicki *et al*. 2016*b*), within the tribe Discocerinini and the monophyly of this group is substantiated by the setulose notopleuron. *Polytrichophora* may be distinguished from the *Discocerina*-group, by the secondary "series" of facial setae (Fig. 41), a character unique to the genus and establishes its monophyly. Adults occur in coastal marine habitats, as well as in freshwater environments. The biology and immature stages otherwise remain unknown. There is currently no identification key to Afrotropical species.

***Psilopa* Fallén** (Discomyzinae: Psilopini)**.** A genus of 43 described species, occurring in all zoogeographical regions, except Antarctica. The Old World fauna is more diverse than the New World fauna and the Afrotropical fauna comprises 21 species widely distributed in the continental Afrotropics, as well as Cabo Verde, the Indian Ocean islands of Madagascar and Seychelles and Yemen in the Southern Arabian Peninsula. The biology and immature stages are poorly known, but phytophagy is suspected. There is currently no identification key to Afrotropical species.

***Psilopoidea* Cresson** (Hydrelliinae: Typopsilopini)**.** Currently an endemic monotypic genus, with the single described species, *P. howardi* Cresson, 1939, recorded from Democratic Republic of Congo, Malawi, Mozambique and Rwanda. A second, undescribed species is known from Madagascar. Specimens are rare in collections. Two synapomorphies characterise the genus and establish its monophyly within the tribe Typopsilopini: paravertical setae well-developed, distinctly inclinate (Fig. 69) and the number of dorsocentral setae 4 (1 + 3), anterior two setae much shorter than posterior two setae. Biology and immature stages remain unknown.

***Ptilomyia* Coquillett** (Hydrelliinae: Atissini)**.** A genus of 14 described species, occurring in all zoogeographical regions, except the Australasian/Oceanian and Oriental Regions and Antarctica. A single species, *P. africana* (Cresson, 1943), occurs in the Afrotropics, recorded from Democratic Republic of Congo, Sierra Leone and South Africa. The dorsal branches of the antennal arista (Fig. 55) distinguish this genus from *Atissa* and both genera frequently occur sympatrically. The genus is associated with saline habitats and to a lesser degree with freshwater environments, the biology and immature stages otherwise remain unknown.

***Rhynchopsilopa* Hendel** (Discomyzinae: Psilopini)**.** A genus of 24 described species (Fig. 5), occurring in the Afrotropical, Oriental and Palaearctic Regions. The genus only occurs in subtropical and tropical zones of the Old World. Fourteen species are recorded from the Afrotropics and are distributed in Central, Southern and West Africa (Wirth 1968*b*). Among psilopine genera, *Rhynchopsilopa* is easily recognised by the greatly elongate postpedicel and rounded abdomen. Adults attack worker ants by mounting the body of an ant and proceeding to feed by forcing the slender, elongate proboscis into a gap between the terminal dorsal and ventral sclerites. Whether feeding results in death of the ant is not known and the relationship may be more parasitic than predaceous (Freidberg & Mathis 1985). The biology and immature stages remain unknown. Afrotropical species can be identified by reference to Wirth (1968*b*).

***Risa* Becker** (Discomyzinae: Risini)**.** A strictly Old World genus of five described species, occurring in the Afrotropical and Palaearctic Regions. A single species, *R. longirostris* Becker, 1907, is currently known from the Afrotropics, described from United Arab Emirates in the Southern Arabian Peninsula. The genus needs revision and the geographic range extends from the Faroe Is. in the north, Spain and Morocco eastward across North Africa, Israel and United Arab Emirates to Mongolia in the Far East. The female terminalia of *Risa* are peculiar and are a primary source of evidence supporting the inclusion of this genus in the Ephydridae. Such terminalia characters are not known to occur in any other family of Schizophora. The genus appears to be restricted to arid regions, where it is associated with host-plants of the family Chenopodiaceae. Biology and immature stages otherwise remain unknown.

***Scatella* Robineau-Desvoidy** (Ephydrinae: Scatellini)**.** A large genus of 138 described species (Fig. 6), occurring in all zoogeographical regions, except Antarctica. Eight species are reported that are widespread in the continental Afrotropics, with species recorded from Ascension Is., Cabo Verde and Saint Helena Is. and from the Indian Ocean islands of Rodrigues Is. and Seychelles. The Afrotropical fauna undoubtedly includes additional undescribed species, however, especially from higher elevations and the genus needs revision. Adults

occur in a diversity of habitats (Foote 1995) and larvae that are known feed on diatoms and other unicellular algae. There is currently no identification key to Afrotropical species.

***Scatophila* Becker** (Ephydrinae: Scatellini)**.** A genus of 55 described species, occurring in all zoogeographical regions, except the Oriental Region and Antarctica. Only three species are currently known from the Afrotropics: *S. eremita* (Frey, 1954), from Tristan da Cunha Is.; *S. minima* (Canzoneri & Meneghini, 1969), from Democratic Republic of Congo and Rwanda; and *S. nilotica* Canzoneri, 1987, from Sudan; but the fauna is largely unknown and undoubtedly numerous species await discovery. Zatwarnicki & Mathis (1994) provided a species-group classification for the genus. Species occur at higher elevations and are usually associated with sandy to muddy shoreline habitats that are largely bare of vegetation and known larvae feed in mud on diatoms and other unicellular algae. There is currently no identification key to Afrotropical species.

***Schema* Becker** (Hydrelliinae: Atissini)**.** A genus of six described species, occurring in the Afrotropical, Nearctic and Palaearctic Regions (Mathis & Zatwarnicki 1995: 59). The genus has never been revised and species are thus difficult to differentiate. Only *S. aldabricum* Mathis & Zatwarnicki, 2003, described from the Aldabra Is. (Seychelles) is known from the Afrotropics. This species is similar to the extralimital species *S. fundatum* (Collin, 1949), but is distinguished from its congeners by characters of the male terminalia. Biology and immature stages remain unknown.

***Scoliocephalus* Becker** (Discomyzinae: Psilopini)**.** An Old World genus of three described species, occurring in the Afrotropical and Palaearctic Regions. Two species are Afrotropical: *S. caboverdensis* Kirk-Spriggs, 1987, described from Cabo Verde; and *S. pallidisetis* Becker, 1903, from United Arab Emirates. Among genera of the tribe Psilopini, *Scoliocephalus* is distinguished by an arista with at most 3 or 4 dorsal branches, moderately geniculate mouthparts (Fig. 85), a well-developed prescutellar acrostichal seta and normal wing venation. Adults are frequently collected on the inflorescences of plants, especially *Tamarix* (Tamaricaceae), that are associated with aquatic habitats, the biology and immature stages otherwise remain unknown. Afrotropical species can be identified by reference to Kirk-Spriggs (1987).

***Setacera* Cresson** (Ephydrinae: Ephydrini)**.** A genus of 15 described species, occurring in all zoogeographical regions, except Antarctica (Mathis 1982). Two species are Afrotropical: the widespread *S. breviventris* (Loew, 1860), recorded from Angola, Kenya and Nigeria in the Afrotropics; and *S. multicolor* (Giordani Soika, 1956), described from Democratic Republic of Congo. They occur primarily in freshwater habitats and most species prefer lentic aquatic systems, especially where a layer

Figs 100.121–123. Immature stages of Ephydridae (all non-Afrotropical): (121) egg of *Hydrellia bergi* Cresson, lateral view; (122) larval habitus of *Notiphila* (*Agrolimna*) sp., lateral view (inset: detail of terminal part); (123) same, *Ephydra* sp. Figs 121–123 (Wirth *et al*. 1987, figs 68–70).

of floating algae has accumulated on the waters' surface. Johannsen (1935: 53) considered the immature stages of *Ephydra* and *Setacera* to be the most highly specialised in the family. These are typical of the tribe Ephydrini, with long, terminal respiratory tubes and eight pairs of short, conical, abdominal prolegs, of which the last pair is the largest, with claws opposable to those of the other prolegs. Afrotropical species can be identified by reference to Mathis (1982).

***Subpelignus* Papp** (Hydrelliinae: Atissini)**.** An Old World genus of two described species, occurring in the Afrotropical and Palaearctic Regions. The only known Afrotropical species, *S. maculipennis* Mathis & Zatwarnicki, 2017, was described from United Arab Emirates in the Arabian Peninsula. The species is distinguished from its congeners on wing venation and structure of the male terminalia. Biology and immature stages remain unknown. The Afrotropical species can be identified by referral to Mathis *et al*. (2017: 678), but as with most other genera of the tribe Atissini, the genus requires revision.

***Trimerogastra* Hendel** (Gymnomyzinae: Gymnomyzini)**.** A genus of four described species, occurring in the Afrotropical, Australasian/Oceanian and Oriental Regions. The single, widespread species, *T. cincta* Hendel, 1914, is recorded from United Arab Emirates in the Afrotropical part of the Arabian Peninsula. The widespread, almost pantropical distribution of this species suggests considerable vagility, perhaps abetted by human commerce. Extralimital species are associated with coastal mangrove or other brackish-water habitats, where specimens can be relatively abundant, the biology and immature stages otherwise remain unknown. Mathis & Zatwarnicki (2004) revised *Trimerogastra* and this paper should be consulted to identify *T. cincta*.

***Typopsilopa* Cresson** (Hydrelliinae: Typopsilopini)**.** A genus of 19 described species, occurring in all zoogeographical regions, except the Oriental Region and Antarctica. Eight species are known from the Afrotropics (Wirth 1968*a*), widely distributed in the continental Afrotropics and in Cabo Verde, Madagascar and Yemen. Although the genus is distinctive, species are homogeneous in external structures and to some extent colour. Thus, dissection and study of structures of the male terminalia are frequently necessary to distinguish species. Adults occur on emergent vegetation and Keiper *et al*. (2001) discovered that one New World species, *T. nigra* (Williston, 1896), occurs as a secondary invader of bulrush and cattails that had first been mined by larvae of the moth, *Bellura obliqua gargantua* (Dyar) (Noctuidae), the biology and immature stages otherwise remain unknown. An identification key to species was provided by Wirth (1968*a*).

***Zeros* Cresson** (Ilytheinae: Ilytheini)**.** A genus of 13 described species, occurring in all zoogeographical regions, except Antarctica. The genus occurs pantropically and eight species occur widely in the continental Afrotropics, including the Indian Ocean islands of Madagascar and Seychelles. The biology and immature stages of species occurring in the tropics, including the Afrotropics, remain essentially unknown. The species, *Z. flavipes* (Williston, 1896), recorded from Democratic Republic of Congo (Mathis & Zatwarnicki 1995), was found in sedge-meadow and mud-shore habitats. There is currently no identification key to Afrotropical species.

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MORMOTOMYIIDAE 101

(Terrible Hairy Flies or Frightful Hairy Flies)

Ashley H. Kirk-Spriggs and Robert S. Copeland

Fig. 101.1. Male of *Mormotomyia hirsuta* Austen (Kenya) (photograph R.S. Copeland).

Diagnosis

Medium-sized flies (body length excluding legs: ♂ 6.50–8.35 mm; ♀ 5.79–6.33 mm), long-legged, stenopterous acalyptrate flies, clothed in dark sepia coloured, extremely long and closely packed setation on entire body and appendages, superficially resembling a solifuge (Figs 1, 8); sexually dimorphic, males larger, with male head (Fig. 2) narrower than female head (Fig. 3), male setation considerably longer than female setation, often with wavy tips (e.g., Fig. 7) and male tarsomere 1 of mid leg prolonged and indented (presumably for clasping female during copulation) (Fig. 6).

Head (Figs 1, 2–4, 8) subquadrate in profile (Fig. 4), face deeply excavated below antennal insertions, lacking all macrochaetae (or setae poorly defined), other than group of strong pseudovibrissal setae at anterior margin; compound eye greatly reduced, elliptical or lozenge-shaped (Fig. 4); ocelli absent; ocellar triangle (Fig. 2) very large, convex (slightly wider in female; Fig. 3); frons with deeply excavated, silver pruinose groove either side of ocellar triangle (Fig. 4); antenna (Fig. 4) pendulous, concolourous with head; pedicel triangular in profile, with lateral seam; postpedicel, narrower, oval; arista long and bare; proboscis (Fig. 4) greatly enlarged and broad in profile; palpus (Fig. 4) spatulate with long setation.

Thorax (Fig. 8) deeper than long, smooth and shiny; lacking transverse suture and all macrochaetae, but clothed in long dense sepia coloured setation. Wings held erect in living flies (Fig. 1); stenopterous (*sensu* Hackman 1964), reduced to

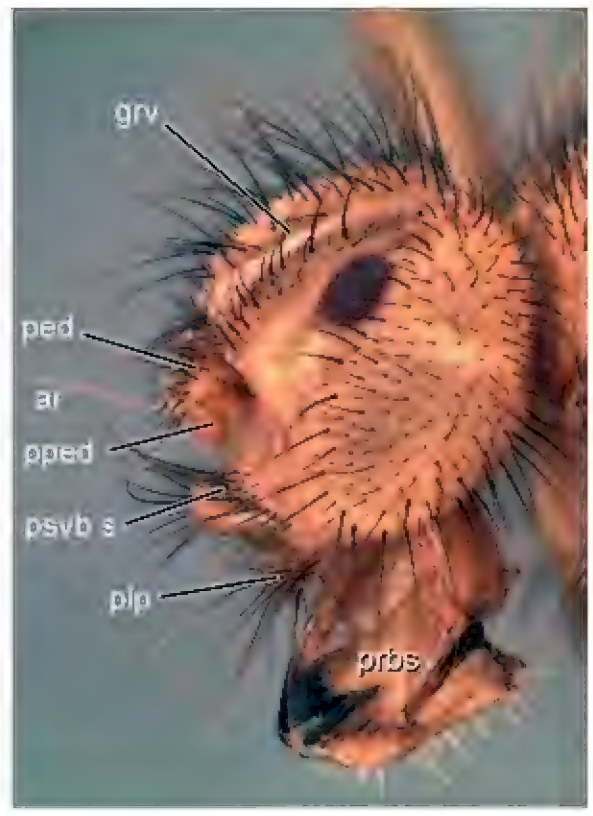
Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2021. Manual of Afrotropical Diptera. Volume 3. Brachycera—Cyclorrhapha, excluding Calyptratae. *Suricata* 8. South African National Biodiversity Institute, Pretoria; pp. 2231–2237.

narrow, slightly curled straps, fringed with long setation (Figs 1, 5, 8), venation reduced to 2 apparent veins; basal sclerites comprising basicosta, tegula and 4 axillary sclerites; costal vein with costagial break (see Kirk-Spriggs *et al*. 2011, fig. 47); halter reduced to short, spinulose nodular process (see Kirk-Spriggs *et al*. 2011, fig. 48). Legs (Figs 1, 6–8) extremely long, shiny, with "knees" often darker pigmented, fringed with fine setation (sometimes forming prominent tufts on fore tibia of male), but lacking macrochaetae, except dorsal surface of tarsomere 5 with preapical, long, curved and prominent seta (Fig. 8); tarsal claws (Figs 6, 8) very large, curved, with blunt tooth at base; pulvillus prominent (Figs 6, 8), with ®Velcro-like overlapping hooks (see Kirk-Spriggs *et al*. 2011, figs 39–41, 42).

Abdomen (Fig. 8) long, parallel-sided, with long setation (as on rest of body); male terminalia (Figs 10–12) conspicuous by absence of moveable surstyli; epandrium (Figs 10, 11) saddle-shaped, enclosing all terminalia structures, other than ventrally extended hypandrium and anteriorly directed

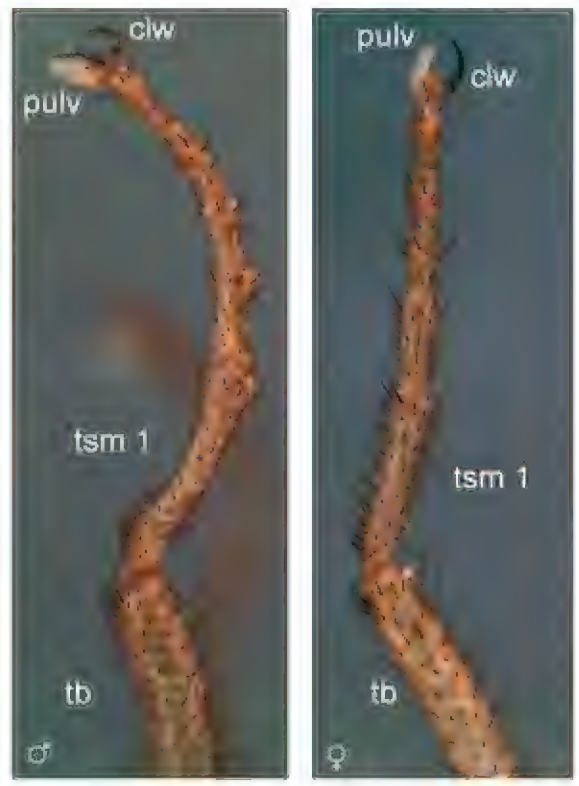
2 *Mormotomyia* ♂

3 *Mormotomyia* ♀



4 *Mormotomyia* ♂

5 *Mormotomyia* ♂

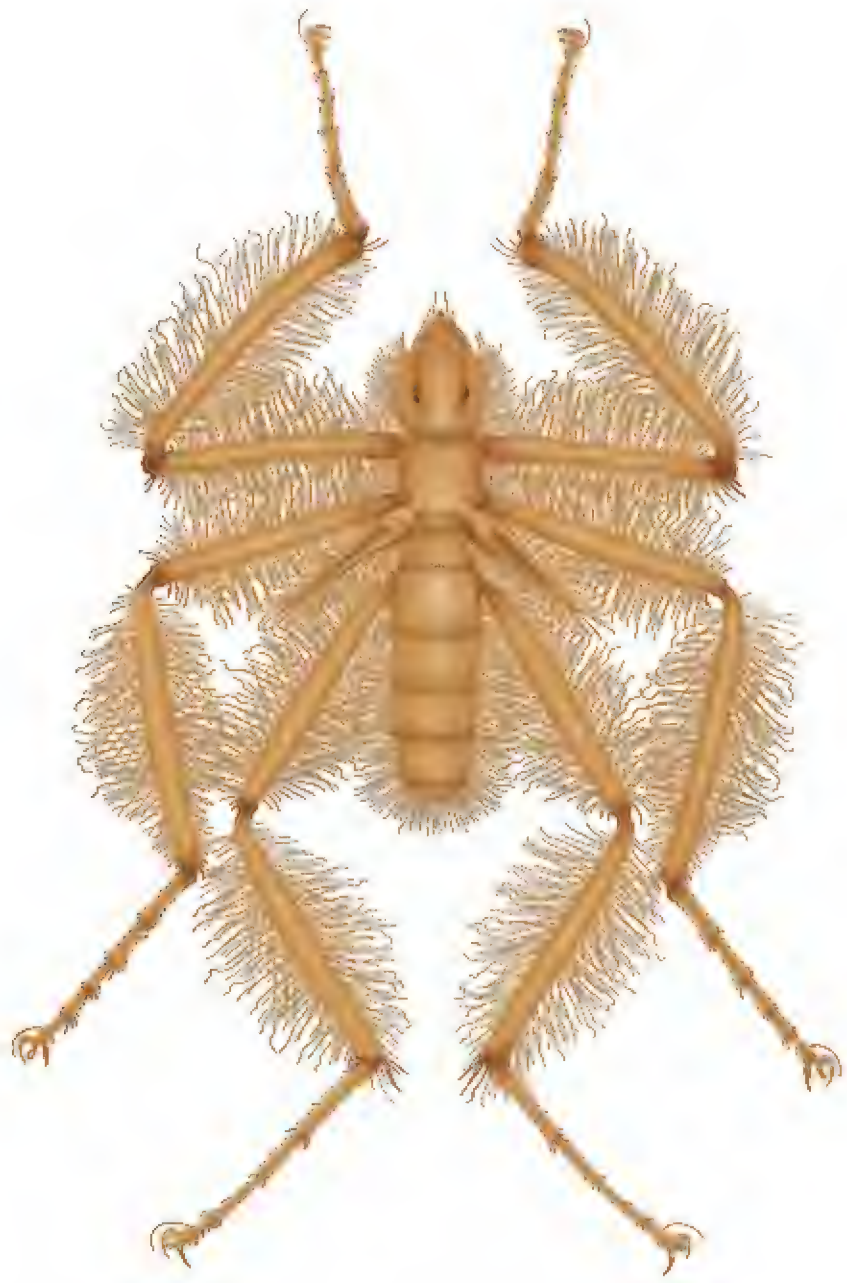


6 *Mormotomyia*

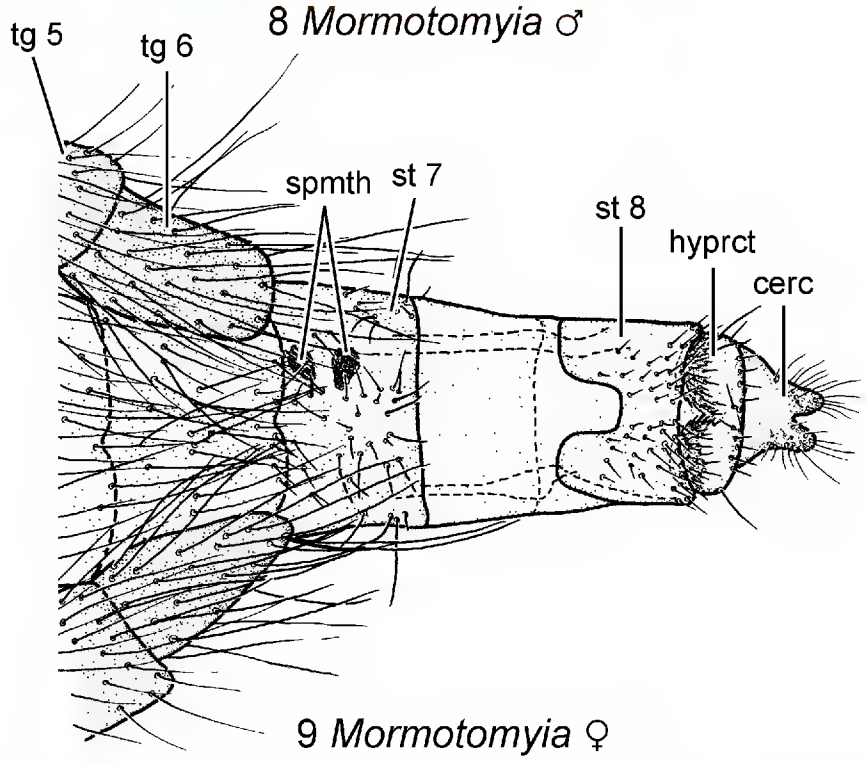
7 *Mormotomyia*

Figs 101.2–7. Heads, wings and legs of Mormotomyiidae: (2) head of *Mormotomyia hirsuta* Austen, dorsal view ♂; (3); same, ♀; (4) same, lateral view ♂; (5) same, wings, dorsal view ♂; (6) same, mid tarsus, lateral view (left) ♂ (right) ♀; (7) same, fore tibia, lateral view (left) ♂ (right) ♀.

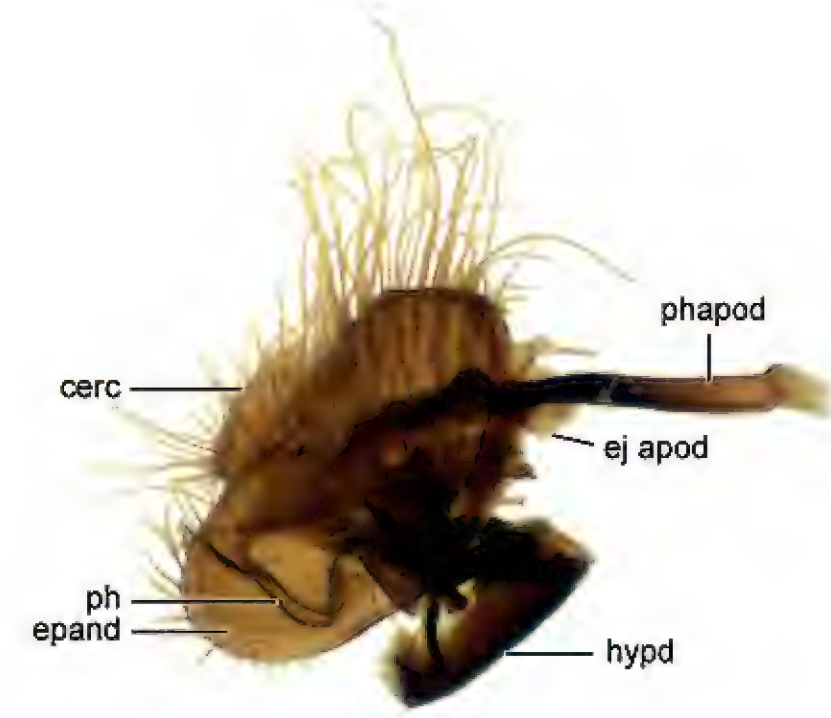
Abbreviations: ar – arista; clw – claw; grv – groove; oc tr – ocellar triangle; ped – pedicel; plp – palpus; pped – postpedicel; prbs – proboscis; psvb s – pseudovibrissal setae; pulv – pulvillus; tb – tibia; tsm – tarsomere; wg – wing.



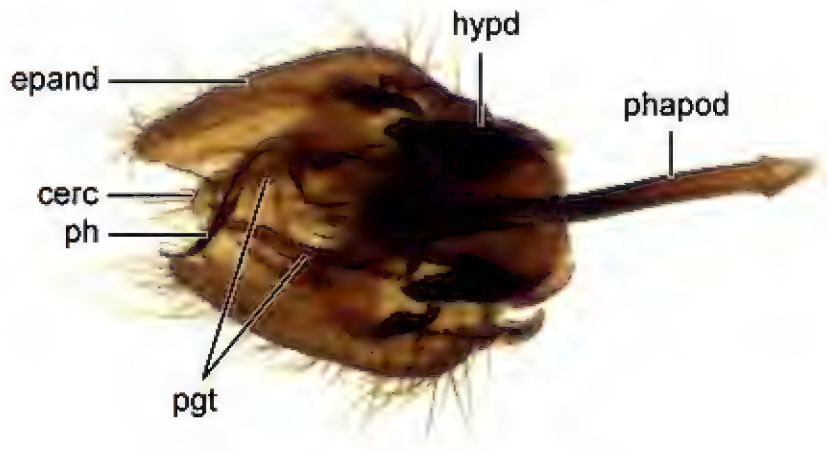
8 *Mormotomyia* ♂



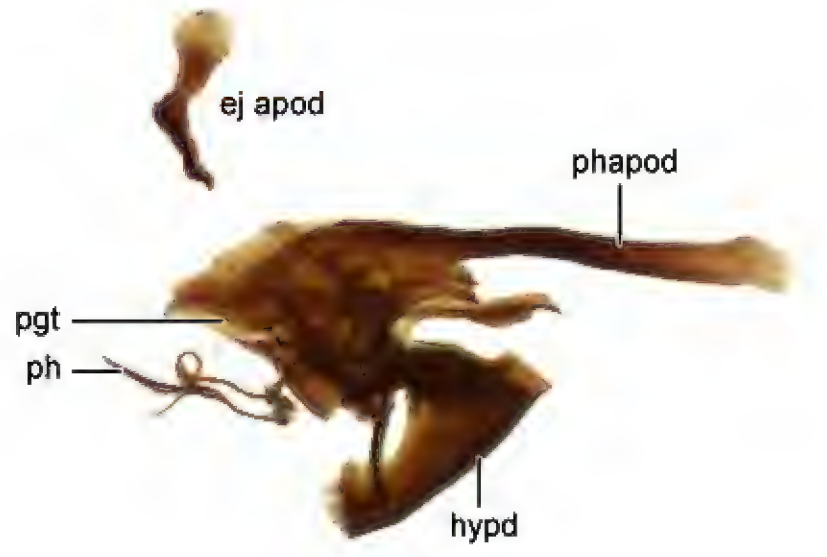
9 *Mormotomyia* ♀



10 *Mormotomyia* ♂



11 *Mormotomyia* ♂



12 *Mormotomyia* ♂

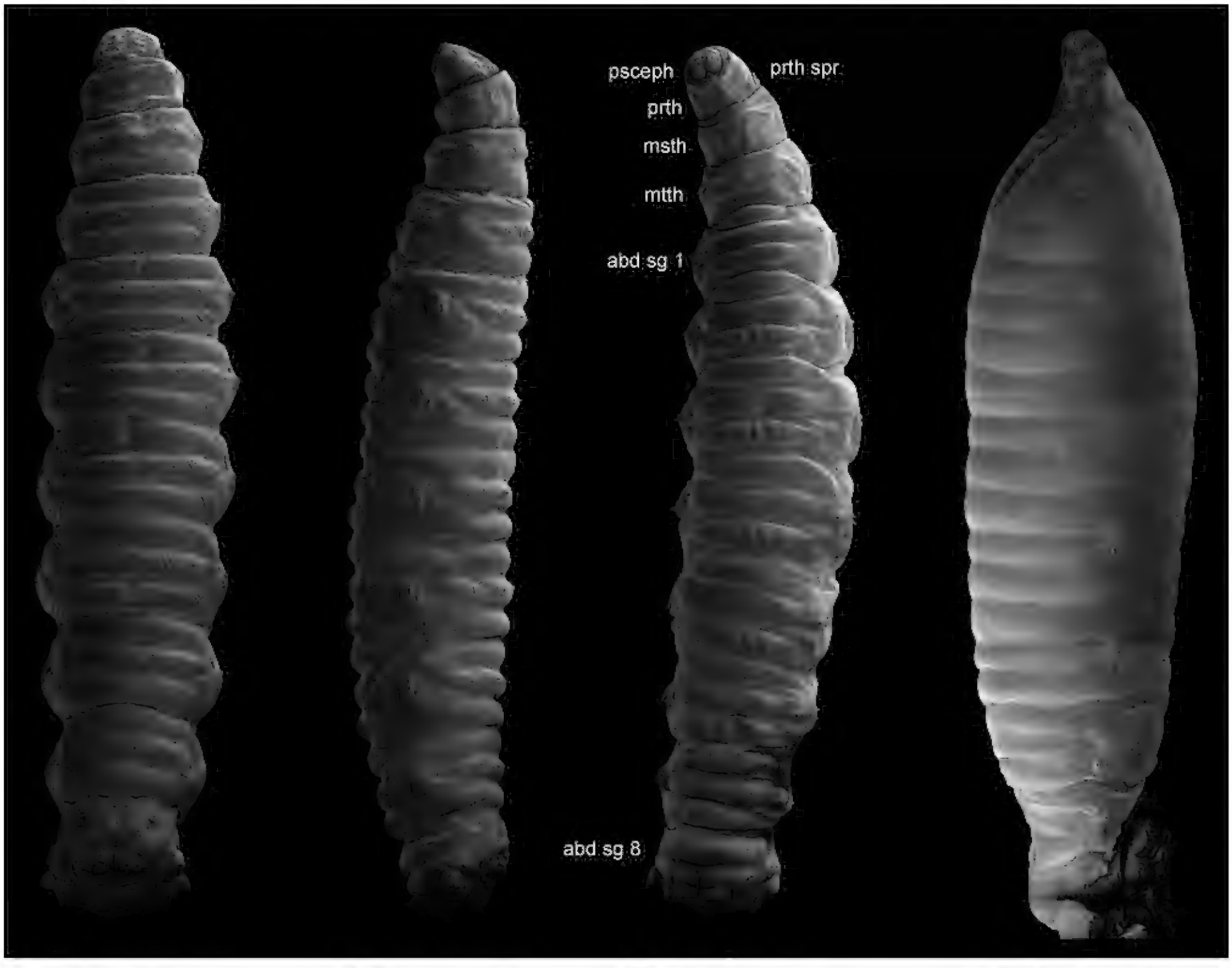
Figs 101.8–12. Habitus, female postabdomen and male terminalia of Mormotomyiidae: (8) habitus of *Mormotomyia hirsuta* Austen, dorsal view ♂; (9) same, female postabdomen, ventral view; (10) same, male terminalia, lateral view; (11) same, ventral view; (12) same, internal male terminalia, lateral view. Fig. 8 (M. van Rensburg, after Austen 1936, fig. 2).

Abbreviations: cerc – cercus; ej apod – ejaculatory apodeme; epand – epandrium; hypd – hypandrium; hyprct – hypoproct; pgt – postgonite; ph – phallus; phapod – phallapodeme; spmth – spermathecae; st – sternite; tg – tergite.

phallapodeme; cercus (Figs 10, 11) long, narrow and flattened, with short setae; hypandrium (Figs 10–12) in form of large, sclerotised plate, extending below epandrium, setose apically; postgonites (Figs 11, 12) narrow, sharp and convergent; phallapodeme (Figs 10–12) long, parallel-sided; phallus (Figs 10–12) divided into two curved linear extensions, setose for part of their length; ejaculatory apodeme (Figs 10, 12) narrow basally, laterally expanded apically, on long ejaculatory duct (not visible on Fig. 12); female abdomen (Fig. 9) with tergites 1–6 clothed in long closely packed setation (as on other body parts); sternites 7 and 8 more weakly sclerotised, quadrate, with much shorter and sparser setation; tergite and sternite 8 indented medially; hypoproct with conspicuous spinose region basally, this indented basomedially; cercus short, fused basally, with fine apical and lateral setulae and pair of prominent divergent setae basomedially on dorsal surface (not visible on Fig. 9); cuticular parts of internal female reproductive tract comprising tubular vagina, 2 sclerotised spermathecae (Fig. 9), paired accessory glands and small 1-chambered sclerotised ventral receptacle (see Kirk-Spriggs *et al*. 2011, figs 30, 31).

Egg (Fig. 17) oval, seed-like (viewed laterally), with ribbed surface, corrugated lateral margin and small micropore.

Third-instar larva (Figs 13–15) cylindrical, slightly flattened; uniformly pure white, except prothoracic and posterior spiracles; body segmentation of usual schizophoran arrangement (Fig. 15), divided into pseudocephalon, three thoracic (prothorax, mesothorax and metathorax) and 8 abdominal segments; creeping welts encircling all body compartments on



Figs 101.13–16. Immature stages of Mormotomyiidae: (13) *Mormotomyia hirsuta* Austen, third-instar larva, dorsal view; (14) same, lateral view; (15) same, ventral view; (16) same, puparium, lateral view. Figs 13–16 (Kirk-Spriggs *et al*. 2011, figs 1–4).

Abbreviations: abd sg – abdominal segment; msth – mesothorax; mtth – metathorax; prth – prothorax; prth spr – prothoracic spiracle; psceph – pseudocephalon.

anterior 1/6; prothoracic spiracles fan-shaped, normally consisting of 18 short, oblong papillae on broad, laterally expanded lobe-like projection; posterior spiracles on extremely short stigmatophores, each with 3 radiating, elliptical, long and narrow spiracular openings in shamrock-shaped cuticular depression; cephaloskeleton (Fig. 18) with mouthhook drawn-out, with posterior dorsal process; dental sclerite positioned below mouthhook; intermediate sclerite H-shaped (Fig. 18), markedly widened in basal 1/3; basal sclerite deep brown-black, divided into dorsal and ventral cornu, with needle-like parastomal bar and dorsal bridge consisting of network of holes.

Puparium (Fig. 16) pale tan-brown in colour; broad, strongly dorsoventrally flattened and markedly wider at anterior end; deep, lateral crease-like indentations (allowing articulation) strongly developed between abdominal segments 5 and 6 and 6 and 7.

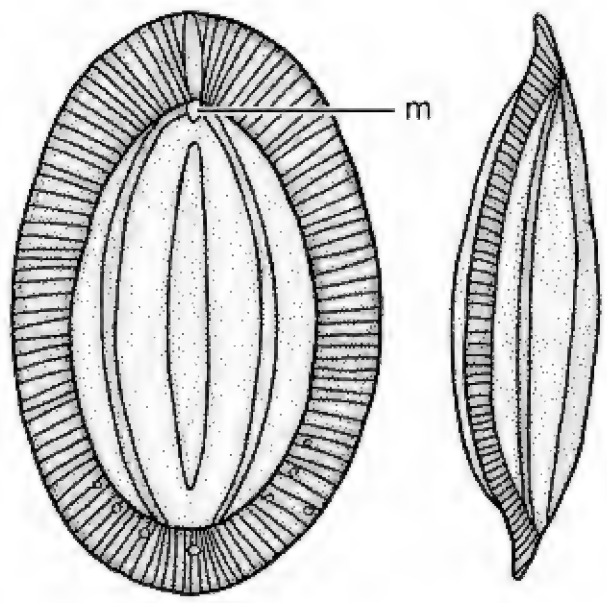
Mormotomyiidae are unlikely to be confused with other families of flies, but some unrelated Scathophagidae (see Chapter 110), have similar long dense sepia coloured setation.

Biology and immature stages

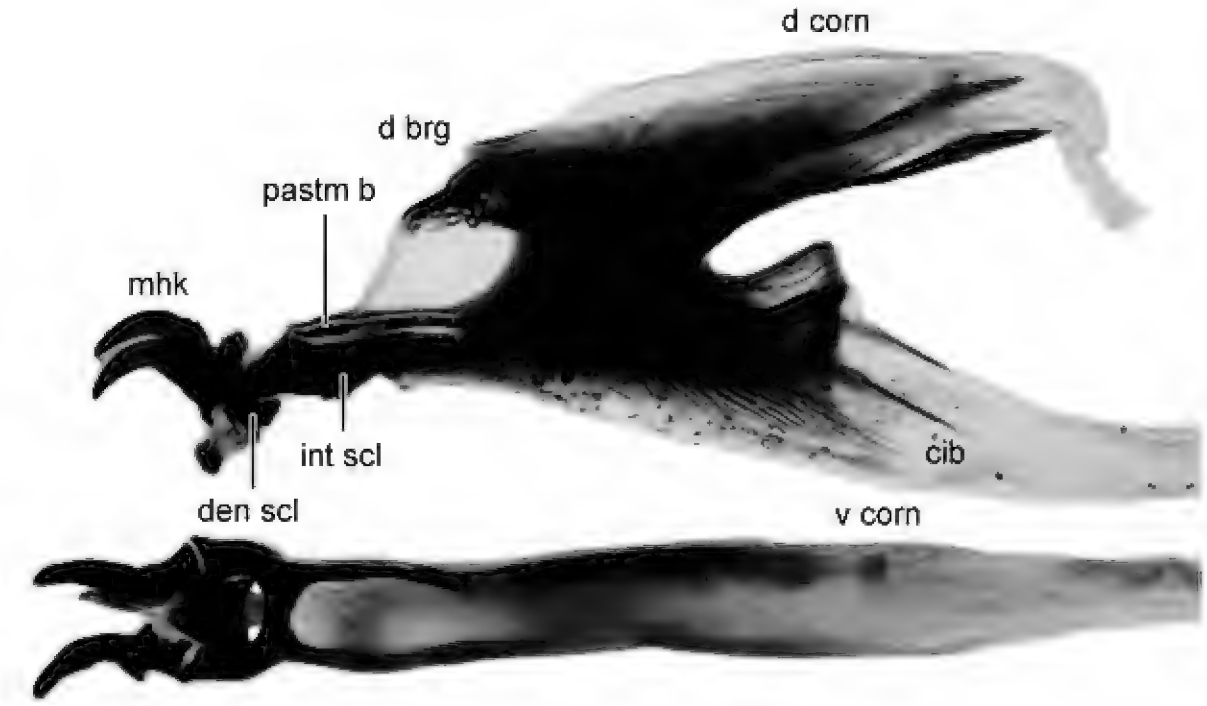
The single described species of the family Mormotomyiidae, *Mormotomyia hirsuta* Austen, 1936, was previously only known from the type locality, Ukasi Hill in eastern Kenya, where it inhabits a cave-like rock cleft that transects the hill from top to bottom and from north to south and a horizontal rock fissure inhabited by roosting insectivorous bats on the northern face of the hill (photographs in Copeland *et al*. 2011; Kirk-Spriggs *et al*. 2011).

Prior to its re-discovery in December 2010, the species had only been collected on two previous occasions; in May 1933 and December 1948, both following heavy rains. On those occasions flies were numerous in the main north-south cleft of the hill, but it appears bat populations may have declined in this cleft and the dominant fly population now resides in a horizontal rock fissure on the northern rock face. Following an extensive survey of caves and horizontal rock fissures inhabited by bats in eastern Kenya, evidence of additional populations were recently discovered at Ngauluka and Makilu Hills, also located in the Ukasi area, and at Mbuinzau Hill, 187 km to the south of the Ukasi hills populations. In all four cases flies were found to inhabit horizontal rock fissures (Copeland *et al*. 2014). Once thought to be the "rarest fly in the world" the conservation status of *Mormotomyia* is probably relatively robust given the extensive areas of similar *Acacia-Commiphora* bushlands and thickets with their numerous inselbergs, rocky hills and mountains.

Sharpe (cited in Austen 1936) noted that the flies "… came floating down from above like feathers" (Austen 1936: 340); a behaviour later noted by Emden (1950), who remarked that the fall is apparently much slowed by the long, shaggy, hair-like body setae and occurs in a slight spiral motion. Adults exhibit a number of features typical of cavernicolous insects, including greatly reduced eyes (Figs 2–4) and wings (Figs 1, 5, 8), absence of ocelli (Figs 2, 3), extremely long legs (Figs 1, 8), elongation of the arista and thickening of the proboscis (Fig. 4), but lack features indicative of a parasitic or phoretic lifestyle on bats or swifts, including a thick leathery cuticle, short stout appendages and acutely toothed tarsal claws exhibited in the parasitic subfamilies Nycteribiinae and the Strebline grade (Hippoboscidae) (see Chapter 109) and phoretic non-Afrotropical Mystacinobiidae (Kirk-Spriggs *et al*. 2011). Although flies occur



17 *Mormotomyia*



18 *Mormotomyia*

Figs 101.17–18. Immature stages of Mormotomyiidae: (17) *Mormotomyia hirsuta* Austen, egg, dorsal view (left) and lateral view (right); (18) same, larval cephaloskeleton, lateral view (above) and dorsal view (below). Fig. 17 (after van Emden 1950, figs 15a, b), Fig. 18 (Kirk-Spriggs *et al*. 2011, fig. 29).

Abbreviations: cib – cibarium; d brg – dorsal bridge; d corn – dorsal cornu; den scl – dental sclerite; int scl – intermediate sclerite; m – micropore; mhk – mouthhook; pastm b – parastomal bars; v corn – ventral cornu.

in the parietal (shaded) zone, the presumed restrictive microclimatic conditions prevalent deep within horizontal fissures, the larval dependency on bat guano and the inability of adults to fly and disperse, coupled with morphological adaptations to a cavernicolous lifestyle, clearly indicate it to be a true troglobite (*sensu* Matile 1994).

The larval stages (Figs 13–15) are saprophagous and develop in guano of insectivorous bats. Skulls of two species of insectivorous bats, namely: *Chaerephon cf. bivittatus* (Heuglin) and *Tadarida aegyptiaca* (E. Geoffroy) (both Molossidae), were identified at the Ukasi Hill site by Copeland *et al*. (2011), who suggested that these are probably the two major guano-producing species responsible for the larval breeding medium. The immature stages were first described by Emden (1950) and were re-described using stereoscan microscopy by Kirk-Spriggs *et al*. (2011). Emden (1950) concluded that flies deposit their flattened, seed-like eggs (Fig. 17) into cracks and crevices in the rock. Guano pellets accumulate during the dry season, either within the main horizontal rock fissures or below it following rainfall events that "wash" guano out of the clefts whereupon they fall and accumulate in depressions below the rock face. Kirk-Spriggs *et al*. (2011) have suggested that the eggs remain dormant for extended periods during the dry season, with rapid larval development being triggered by the onset of the rains. Kirk-Spriggs *et al*. (2011) noted that all examined puparia had a semi-pliable, waxy substance adhering to the posterior end, presumably secreted from the anus during pupariation. Under normal circumstances this substance is probably used to help fix the puparium in an upright position to the ceiling or walls of the rock cleft (see Kirk-Spriggs *et al*. 2011, fig. 52).

Economic significance

Mormotomyiidae have no recorded economic significance.

Classification

The systematic position of Mormotomyiidae has long remained a contentious issue. Austen (1936) considered the family as perhaps distantly related to Sphaeroceridae (as Boroboridae), in the series Acalyptratae. Later, based largely on a study of immature stages, Emden (1950) took a different view, suggesting placement in the Calyptratae and stating (p. 124) "If *Mormotomyia* belongs to the Calyptrata series or is transitional between it and the Acalyptrata, there can be little doubt that the Cordyluridae [= Scathophagidae] are its closest allies." Both Hennig (1971: 63–69) and Griffiths (1972: 226) treated the position of Mormotomyiidae in some detail. Notably, Hennig (1971) mentioned the presence of the seam of the pedicel and suggested that this was not necessarily compelling evidence for its inclusion in the Calyptratae. He extensively discussed the male and female terminalia and noted the presence of two spermathecae in the female. Pont (1980: 713) was the first to place this family in the superfamily Muscoidea and summarised the systematic positions of Austen, Emden and Hennig (1971).

Subsequent authors, however, have been in agreement as to its placement in the "Acalyptratae". Griffiths (1972: 226) interpreted the Mormotomyiidae as an aberrant family in his "prefamily" Tephritoinea. He aligned *Mormotomyia* with the genera *Neossos* Malloch (= *Chiropteromyza* Frey) and *Prosopantrum* Enderlein (= *Cnemospathis* Enderlein), both of which were later transferred to the Heleomyzidae (Sphaeroceroidea) (McAlpine 1985). In the most recent published interpretation, McAlpine (1989: 1485) concluded that the majority of morphological character states indicated placement in the Acalyptratae, provisionally regarding it as a separate family in the Sphaeroceroidea, probably near the Heleomyzidae. McAlpine (2007), however, found no character state which aligned the Mormotomyiidae with the Heteromyzoidea rather than the Muscoidea (or calyptrates) and noted that the deeply cleft pedicel excluded it from the Heteromyzoidea.

Kirk-Spriggs *et al*. (2011) concluded that the structure of the reproductive tract of Mormotomyiidae lends support to the inclusion of that family in the Ephydroidea and later McAlpine (2011) further noted that the general structure of the antenna concurs with this. The collection of suitably preserved specimens in 2010 has now enabled a detailed study of its systematic position using molecular markers (Wiegmann *et al*. in prep.). Results of this study confirm placement of the Mormotomyiidae in the Ephydroidea, as sister to the remainder of the Ephydroidea, except the Ephydridae.

Identification

Mormotomyia hirsuta is easily recognised by the general habitus, setulose appearance, reduced eyes and wings and the extremely long legs. Living flies have a characteristic rapid running motion. Adults should be micro-pinned in the field for subsequent double-mounting (see Chapter 2).

Synopsis of the fauna

***Mormotomyia* Austen.** Only a single species, *M. hirsuta*, is known, which is confined to the Afrotropical Region, making this one of Africa's "flagship" species. It is readily identified with the above diagnosis and by reference to Austen (1936), Emden (1950) and the more recent papers by Kirk-Spriggs *et al*. (2011) and Copeland *et al*. (2011).

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CAMILLIDAE 102

(Camillid Flies)

David A. Barraclough and Ashley H. Kirk-Spriggs

Fig. 102.1. Male of *Afrocamilla* sp. (South Africa) (photograph © S.A. Marshall).

Diagnosis

Small-sized (body length: 2.0–4.0 mm) acalyptrate flies, variable in colour, shiny black, with blue to purple reflections (Fig. 1), brown, or yellow-brown to pallid yellow.

Head (Figs 1–5) with frons invariably with 1 strong reclinate fronto-orbital seta, often with 1 strong proclinate seta, these setae well-separated, with very short anterior reclinate seta usually present in between (Fig. 3); ocellar setae well-developed, proclinate and diverging; postocellar setae reduced and convergent; face without carina; antenna with postpedicel decumbent and typically evident in profile; arista short to long plumose (with dorsal branches significantly longer) (Fig. 4), or bare to pubescent (*Katacamilla* Papp) (Fig. 5); gena with 1 or 2 strong vibrissae; palpus well-developed; proboscis short.

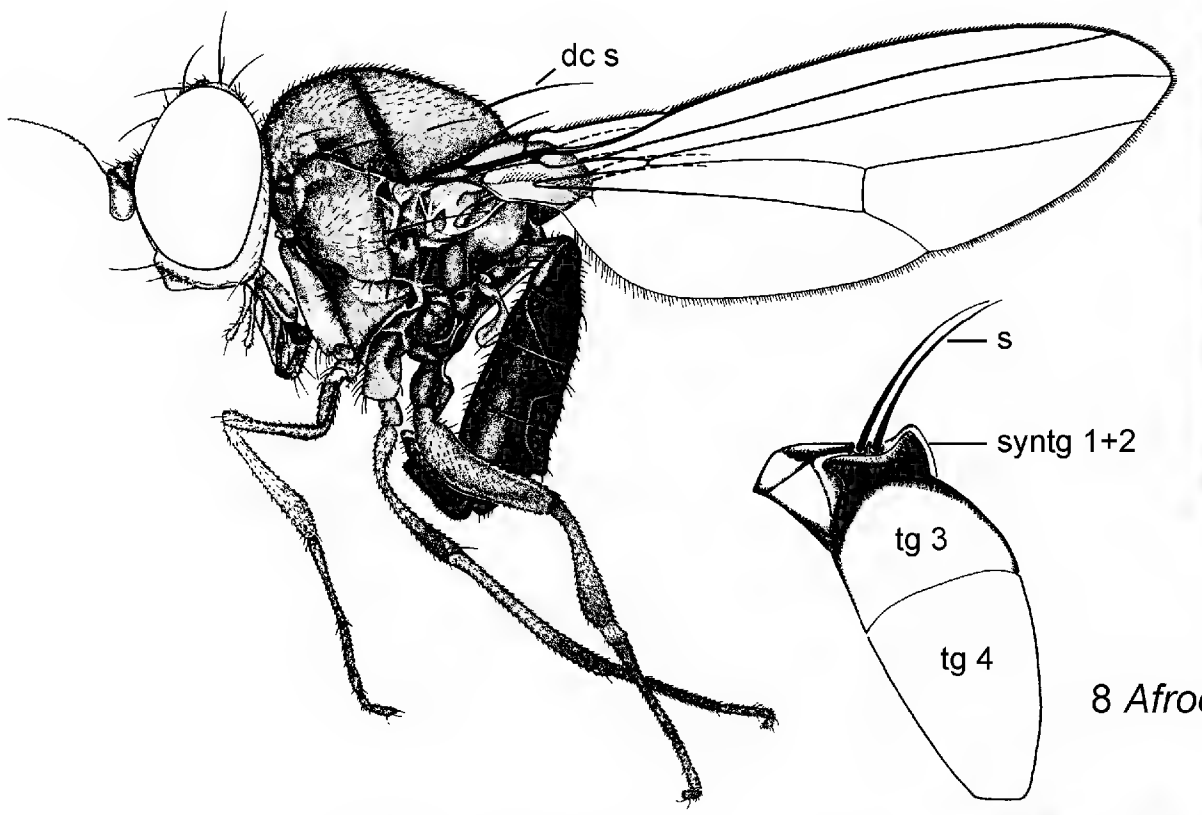
Thorax with 1 postpronotal seta; 2 notopleural setae; 1 (*Katacamilla*) or 2 dorsocentral setae; 1 supra-alar seta; 1 or 2 postalar setae; 4 scutellar setae; scutellar disc bare, or with short setulae (*Katacamilla*); at least 1 strong anepisternal seta; 1 strong, dorsally directed katepisternal seta. Wing (Figs 6, 7) typically narrow, mostly hyaline, but with variously developed dark, transverse fascia in *Afrocamilla* Barraclough and *Teratocamilla* Barraclough (Fig. 6); costal vein (*C*) with humeral and subcostal breaks; subcostal vein (*Sc*) incomplete (evanescent apically); crossvein *bm–m*, vein *CuA+CuP* and cell *cua* absent (Fig. 7). Legs (Figs 1, 2) with fore femur with or without anteroventral spine; apicoventral ctenidium sometimes present

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2021. Manual of Afrotropical Diptera. Volume 3. Brachycera—Cyclorrhapha, excluding Calyptratae. *Suricata* 8. South African National Biodiversity Institute, Pretoria; pp. 2239–2246.

and variously developed; mid tibia with or without dorsal preapical seta.

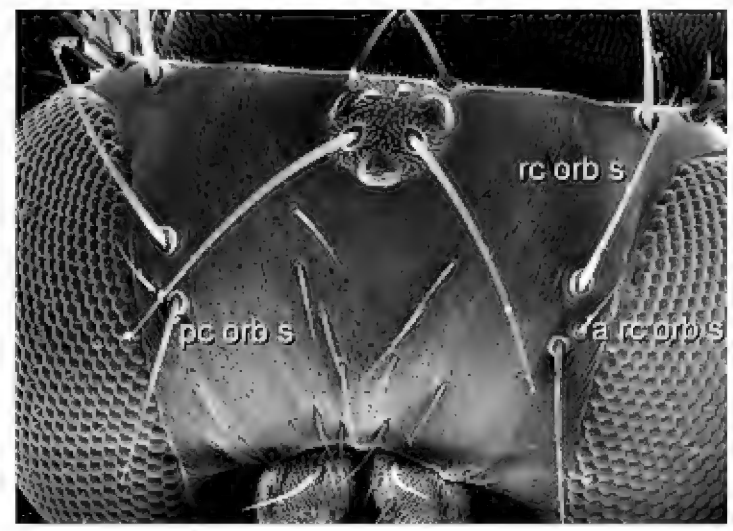
Abdomen (Figs 1, 2) narrow (shiny and metallic in *Afrocamilla* and *Teratocamilla*); syntergite 1 + 2 with pair of prominent, long, marginal setae (*Afrocamilla* and *Teratocamilla*) (Fig. 8), sometimes present; male terminalia (Figs 10, 11) diverse in form; epandrium narrow; surstylus simple; distiphallus long, membranous and symmetrical (Fig. 10), but epandrium broad, surstylus partially fused with epandrium and distiphallus enlarged, prominent and asymmetrical in *Katacamilla* (Fig. 11); female postabdomen telescopic; cerci distinct (partially fused in *Katacamilla*, Fig. 9); 2 spermathecae present, sometimes unsclerotised (Fig. 9); ventral receptacle well-developed (present, but reduced in *Katacamilla*).

The third-instar larva and puparium of *Katacamilla cavernicola* Papp, 1978, have been described in detail by Kirk-Spriggs

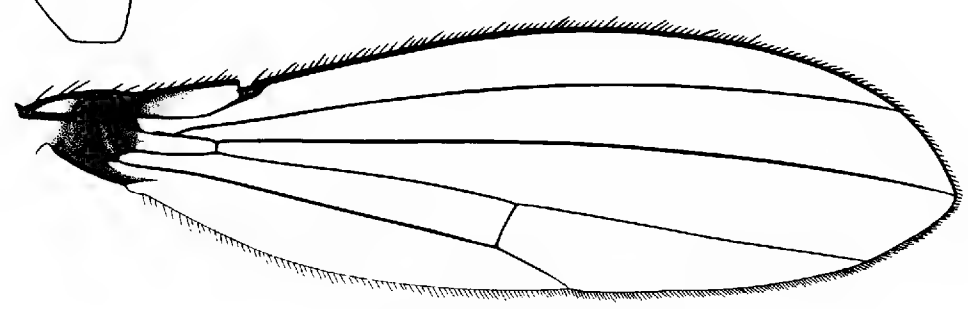


2 *Katacamilla* ♂

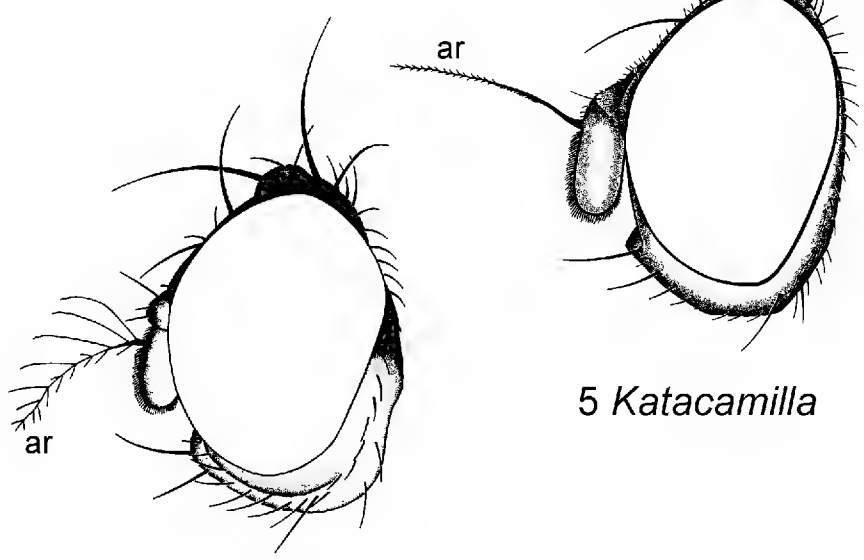
8 *Afrocamilla*



3 *Afrocamilla*

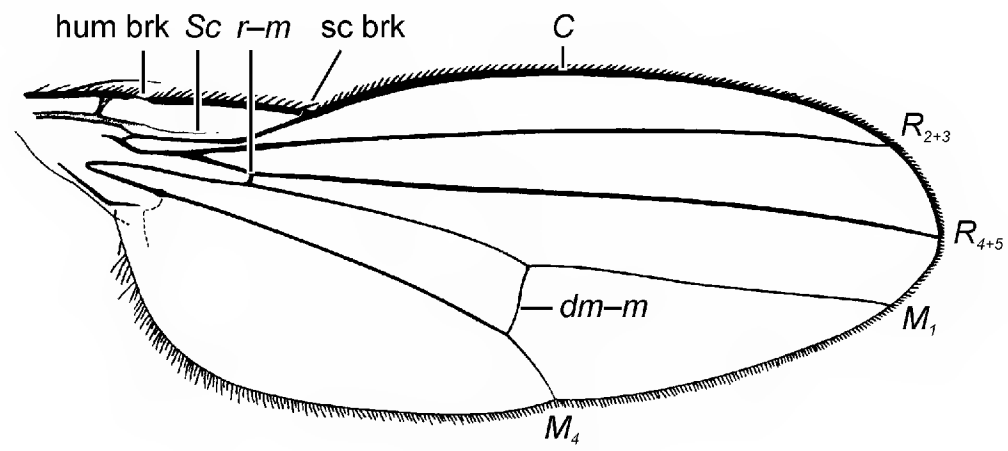


6 *Afrocamilla*



4 *Afrocamilla*

5 *Katacamilla*



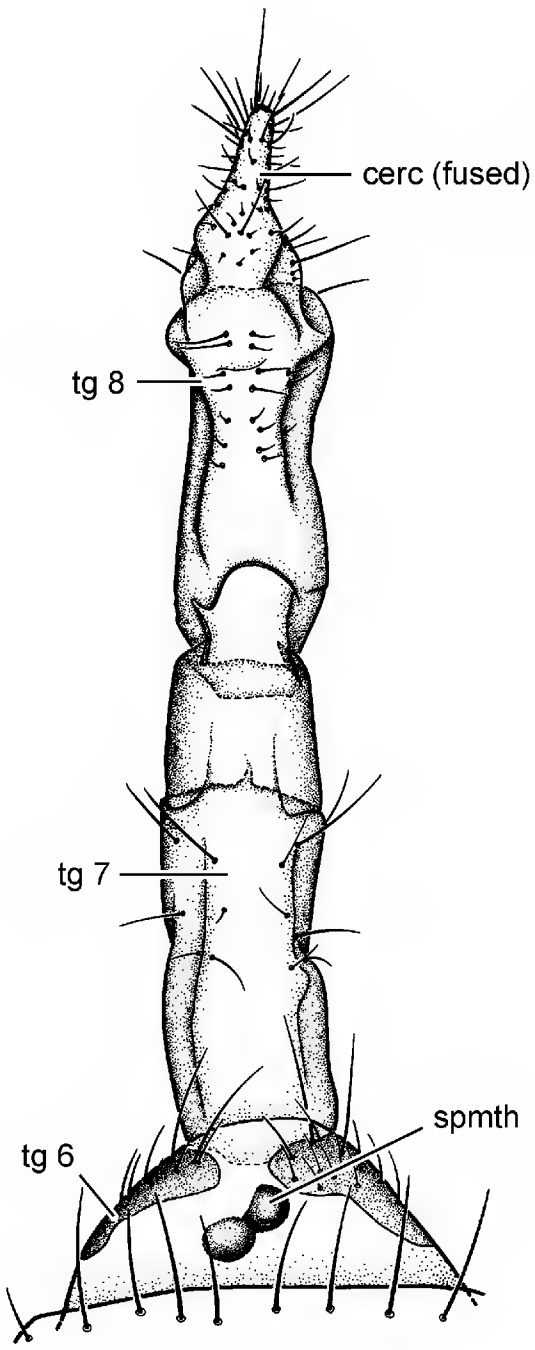
7 *Katacamilla*

Figs 102.2–8. Habitus, frons, heads, wings and abdomen of Camillidae: (2) habitus of *Katacamilla cavernicola* Papp, lateral view; (3) stereoscan micrograph of frons of *Afrocamilla stuckenbergi* Barraclough, dorsal view; (4) head of *A. confusa* Barraclough, lateral view; (5) same, *K. procavia* Barraclough; (6) wing of *A. artopenna* Barraclough, dorsal view; (7) same, *K. cavernicola* Papp; (8) abdomen of *A. stuckenbergi* Barraclough. Figs 2, 5, 7 (Barraclough 1998, figs 1, 9, 3, respectively), Figs 4, 6 (Barraclough 1997*b*, figs 10, 5, respectively), Fig. 8 (Barraclough 1993, fig. 3).

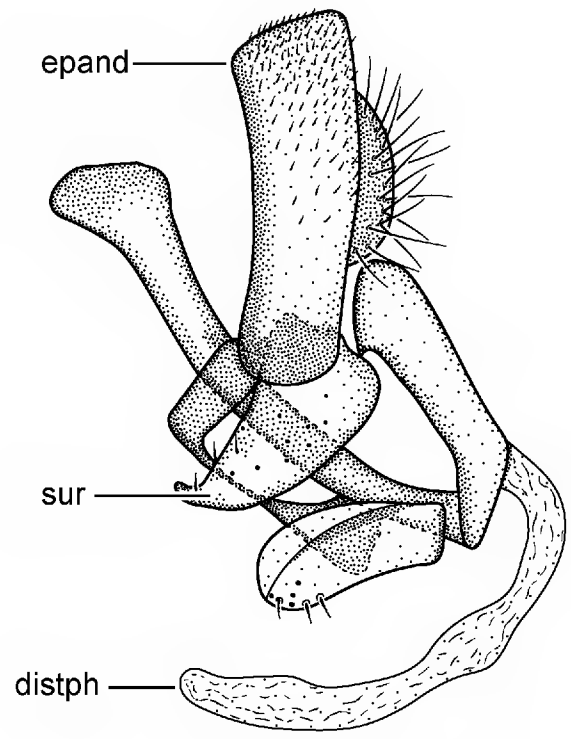
Abbreviations: a rc orb s – anterior reclinate orbital seta; ar – arista; *C* – costal vein; dc s – dorsocentral seta; *dm–m* – discal medial crossvein; hum brk – humeral break; M_1 – first branch of media; M_4 – fourth branch of media; pc orb s – proclinate orbital seta; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; rc orb s – reclinate orbital seta; *r–m* – radial–medial crossvein; s – seta; *Sc* – subcostal vein; sc brk – subcostal break; syntg – syntergite; tg – tergite.

et al. (2002); the immature stages of other genera remain undescribed. Third-instar larva (Fig. 13) narrow, cylindrical, 4.4–4.7 mm in length, of usual schizophoran type; 7 paired tubercles and 1 unpaired tubercle on last abdominal segment; creeping welts (Figs 13, 17) on posterior ⅓ of segments, consisting of multiple rows of short, reclinate spicules, elevated on abdominal segments 3–6; pseudocephalon (Figs 14, 15) separated from prothoracic segment by fold covered with long, pointed, reclinate spicules; pseudocephalon anteriorly distinctly bilobed; labial lobe large; antenna in terminal position; maxillary palpus posteroventral to antenna; prothoracic spiracles (Fig. 16) of fan type, with 4 or 5 long, thin papillae; Keilin's organs (Fig. 18) closely approximated on prothorax; posterior spiracle (Fig, 19) with 3 slit-like, radial spiracular openings, separated by 4 peristigmatic tufts inserted close to rim, each with large, round basal sheet, with a few narrow setulae radiating terminally, ecdysial scar large; cephaloskeleton (Fig. 20) with mouthhooks elongate, sickle-shaped; intermediate sclerite club-shaped; parastomal bars running adjacent and dorsal to intermediate sclerite; basal sclerite with dorsal and ventral cornua subdivided; cuticular sieve comprising network of holes present. Puparium (Fig. 21) 2.90 mm in length; uniform orange-brown, surface subshiny; broad, cylindrical, gently curved at sides.

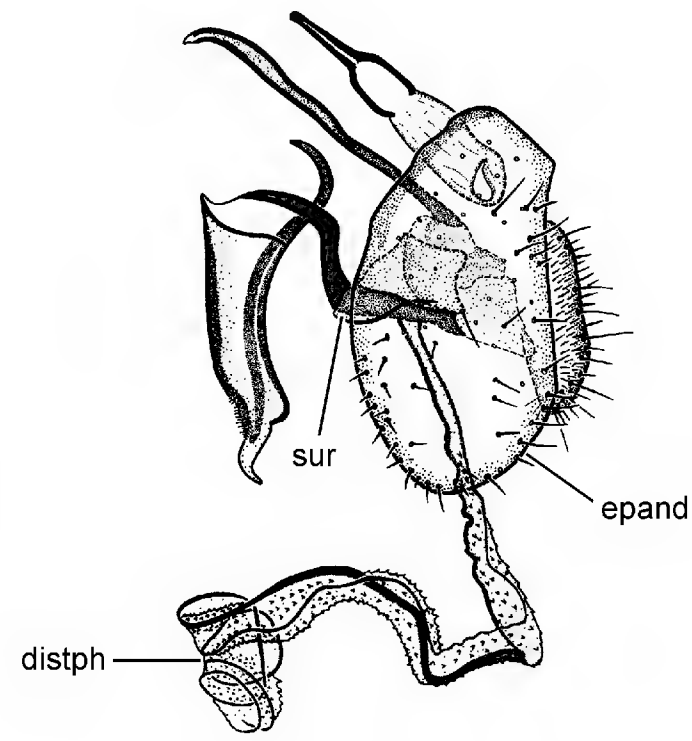
Characters distinguishing Camillidae from other families in the Afrotropical Region include: the size, number and orientation of strong fronto-orbital setae (1 or 2 present, never laterocline); convergent postocellar setae; anepisternum with a distinct seta; wing with 2 costal breaks and subcostal vein evanescent apically; and crossvein *bm–m* and cell *cua* absent. Camillidae may be confused with some Drosophilidae (see Chapter 106), but are immediately distinguished by the presence of an obvious, strong anepisternal seta.



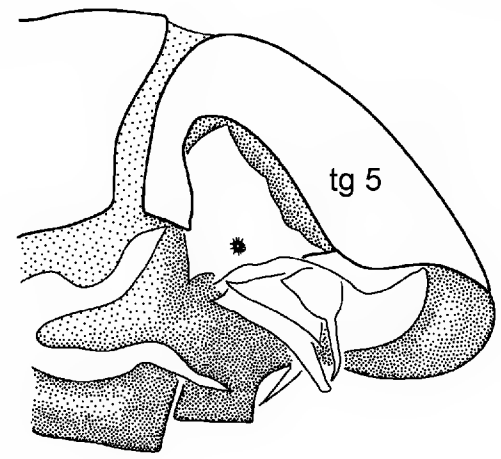
9 *Katacamilla* ♀



10 *Afrocamilla* ♂



11 *Katacamilla* ♂



12 *Teratocamilla* ♂

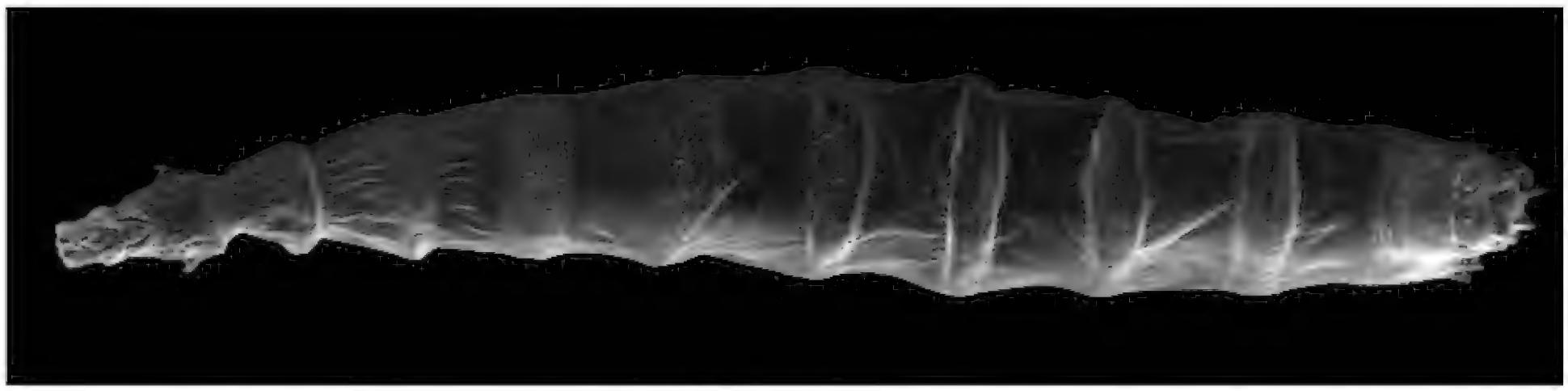
Figs 102.9–12. Female postabdomen and male terminalia of Camillidae: (9) female postabdomen of *Katacamilla procavia* Barraclough, dorsal view; (10) male terminalia of *Afrocamilla armata* (Hackman), lateral view; (11) same, *K. procavia*; (12) same, *Teratocamilla sineseta* Barraclough, oblique posteroventral view. Figs 9, 11 (Barraclough 1998, figs 16, 25), Fig. 10 (after Barraclough 1997*b*, fig. 23), Fig. 12 (after Barraclough 1993, fig. 3).

Abbreviations: cerc – cerci (fused); distph – distiphallus; epand – epandrium; spmth – spermatheca; sur – surstylus; tg – tergite.

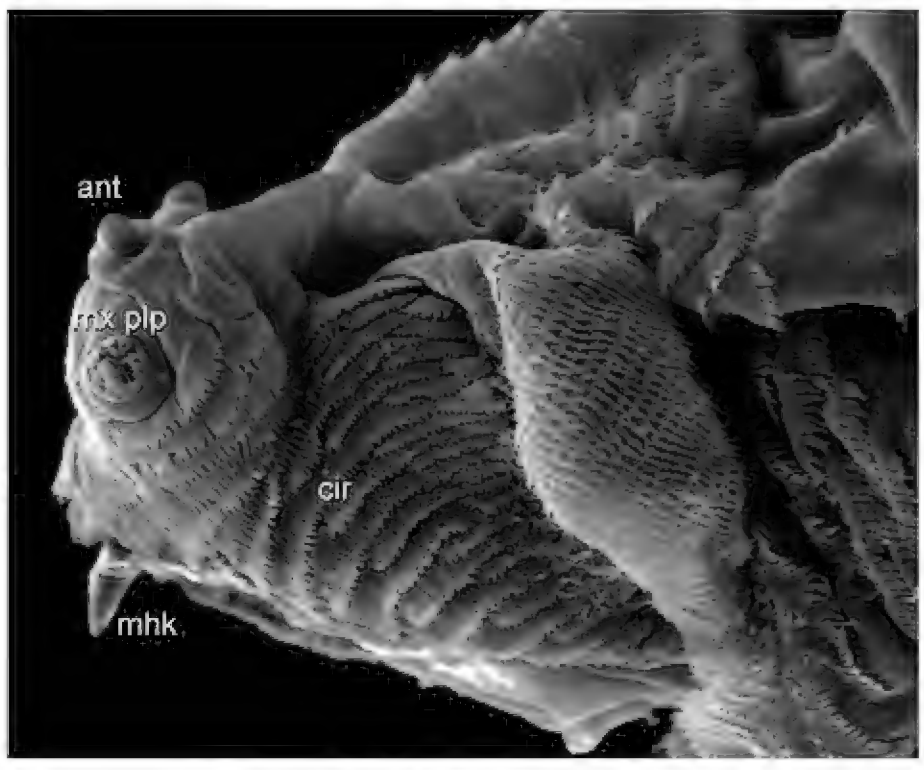
Biology and immature stages

Camillidae are largely coprophagous/guanobious and are associated with the droppings and dung of small mammals (including bats), but also of baboons, monkeys and birds (Barraclough 1997*a*). At least one South African species of *Afrocamilla*, however, is likely to be saprophagous and associated with the rotting and fallen fruit of *Barringtonia* trees (Lecythidaceae) (Barraclough 1998*b*), while *Afrocamilla* sp. nr *artopenna* Barraclough, 1997 and *Katacamilla gallagheri* Barraclough, 1998, are possibly associated with fruit in Yemen (Barraclough 2004). The genus *Katacamilla* contains two described species that are troglophilous (one also parietal). *Katacamilla cavernicola* has been reared from the guano of the Speckled pigeon, *Columba guinea* L. (Columbidae) and the Egyptian slit-faced bat, *Nycteris thebaica* Geoffroy (Nycteridae) in Namibia (Kirk-Spriggs *et al*. 2002), *K. procavia* Barraclough, 1998, has been reared from droppings of the Rock hyrax, *Procavia capensis* (Pallas) (Procaviidae) in Namibia, while the South African species *K. braacki* Barraclough, 1998, has been collected near guano of the Egyptian fruit bat, *Rousettus aegyptius* (Geoffroy) (Pteropodidae) (Barraclough 1998*a*). An undescribed species of *Katacamilla* from eastern Kenya (parietal) has been reared from accumulated guano of the Spotted free-tailed bat, *Chaerephon* cf. *bivittatus* (Heuglin) and the Egyptian free-tailed bat, *Tadarida aegyptiaca* (Geoffroy) (both Molossidae) (A.H. Kirk-Spriggs, pers. obs.).

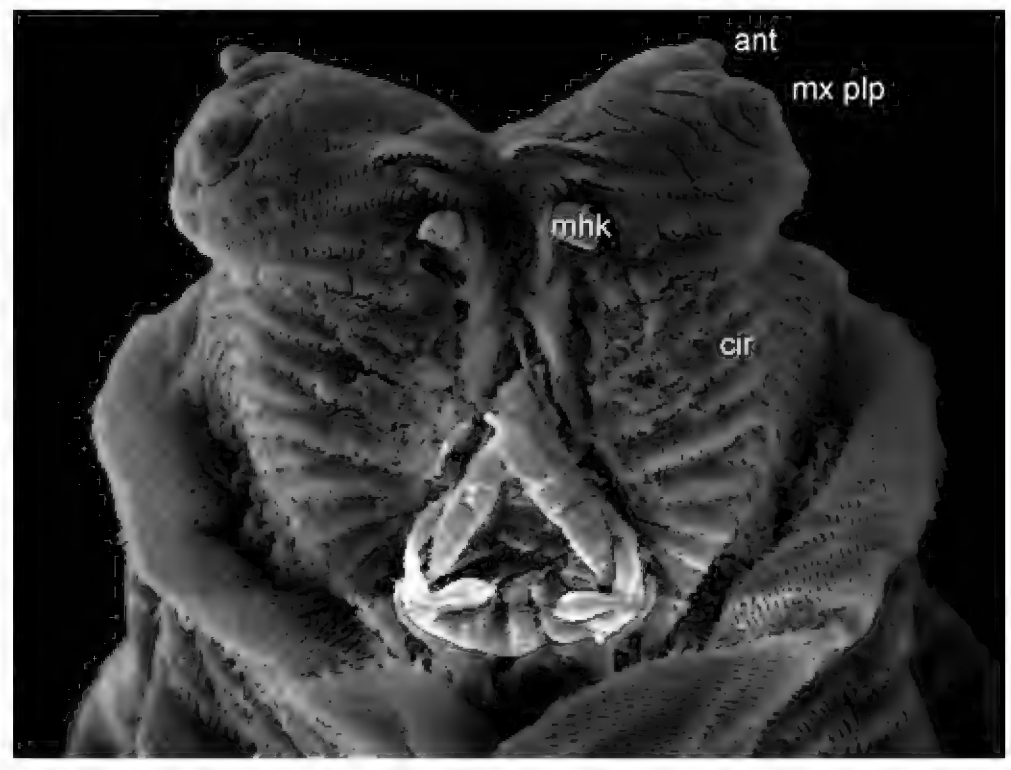
Katacamilla females have been observed hovering above accumulations of bat guano in Kenya, ovipositing either directly into guano, or onto twigs and other embedded debris (A.H. Kirk-Spriggs, pers. obs.). A study of the biology and immature stages of *K. cavernicola* (Kirk-Spriggs *et al*. 2002), revealed that following oviposition, eggs remain dormant in guano for extended periods (up to 6 months) and larval development is triggered, either by precipitation, or perhaps by the urine of bats. Larval development lasts only 7 days and the puparial stage 6–7 days under laboratory conditions. Long series of *Katacamilla* have been sampled using light traps on the Brandberg massif, Namibia, following periods of heavy precipitation (A.H. Kirk-Spriggs, pers. obs.).



13 *Katacamilla*



14 *Katacamilla*



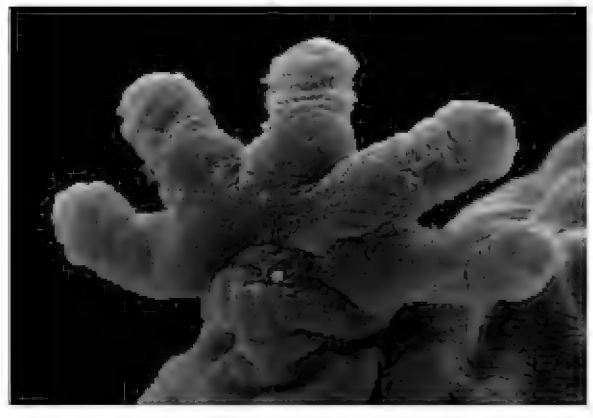
15 *Katacamilla*

Figs 102.13–15. Immature stages of Camillidae: (13) habitus of third-instar larva of *Katacamilla cavernicola* Papp, ventral view; (14) same, pseudocephalon, lateral view; (15) same, ventral view. Figs 13, 15 (after Kirk-Spriggs *et al*. 2002, figs 6, 7), Fig. 14 (courtesy R. Meier).

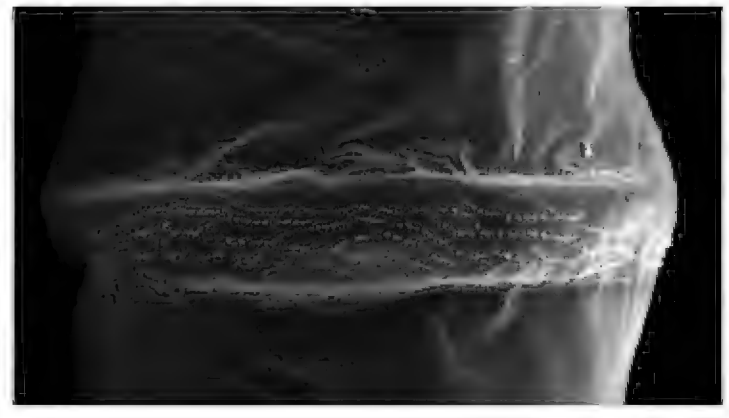
Abbreviations: ant – antenna; cir – cirri; mhk – mouthhook; mx plp – maxillary palpus.

Much of our knowledge of the biology of Camillidae derives from studies on *Afrocamilla* in South Africa (Barraclough 1992, 1997*b*). Species of *Afrocamilla* are frequently strongly associated with the latrines of the Rock hyrax, which typically dwell in large colonies in highly inaccessible areas, such as cliff tops, crevices and rocky outcrops. Adult flies can be readily collected into small vials from the surface of droppings, which are typically found in large quantities beneath overhangs. The paucity of African Camillidae in collections prior to 1992 may be due to the inaccessible nature of these micro-habitats. Most observations are on *A. stuckenbergi* Barraclough, 1992, which typically sits on the upper surfaces of moist, fresh dung pellets, from which the species has been reared in the laboratory (Barraclough 1992). Adults have been observed copulating on pellets and sometimes hover above latrines during short erratic flights (Barraclough 1992). Up to four species of *Afrocamilla* have been collected sympatrically from droppings at the same site (Barraclough 1997*b*) in South Africa and sympatry has also been noted in East Africa (Barraclough 1997*a*).

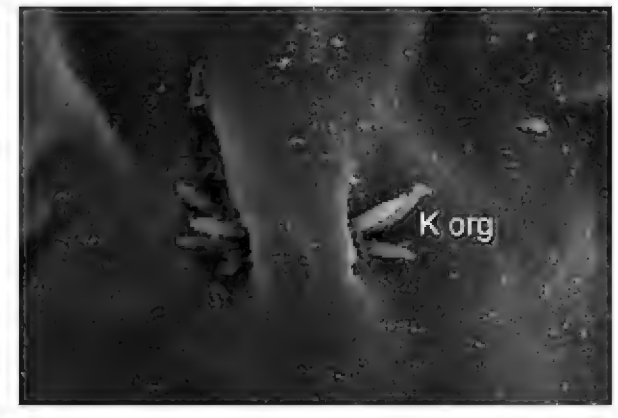
A notable behaviour of *Afrocamilla* adults is the characteristic wing and abdominal movements (Barraclough 1992). Whilst walking on the surface of dung pellets, the elongate, paired marginal setae on syntergite 1 + 2 are flexed upwards



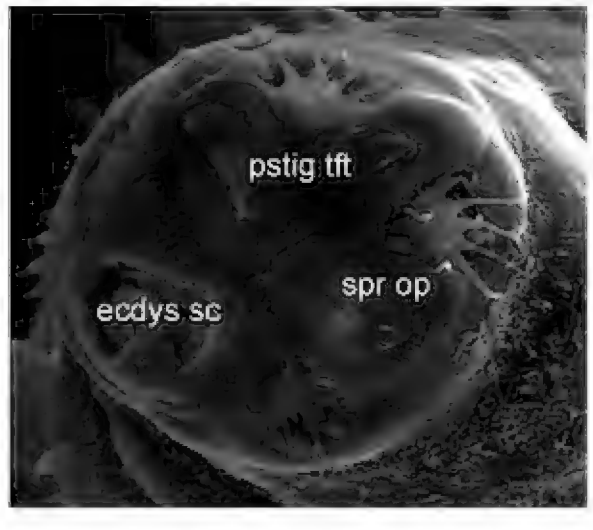
16 *Katacamilla*



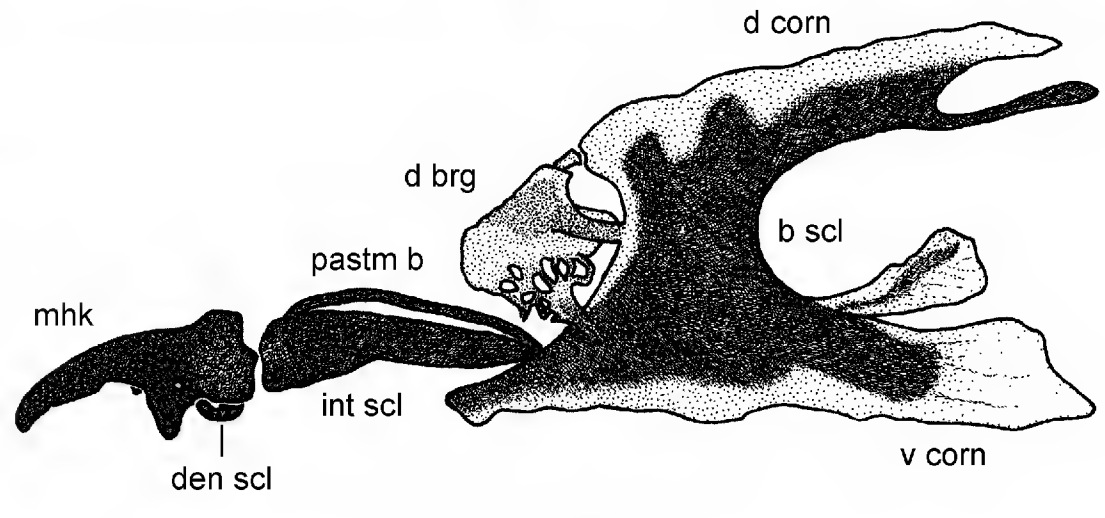
17 *Katacamilla*



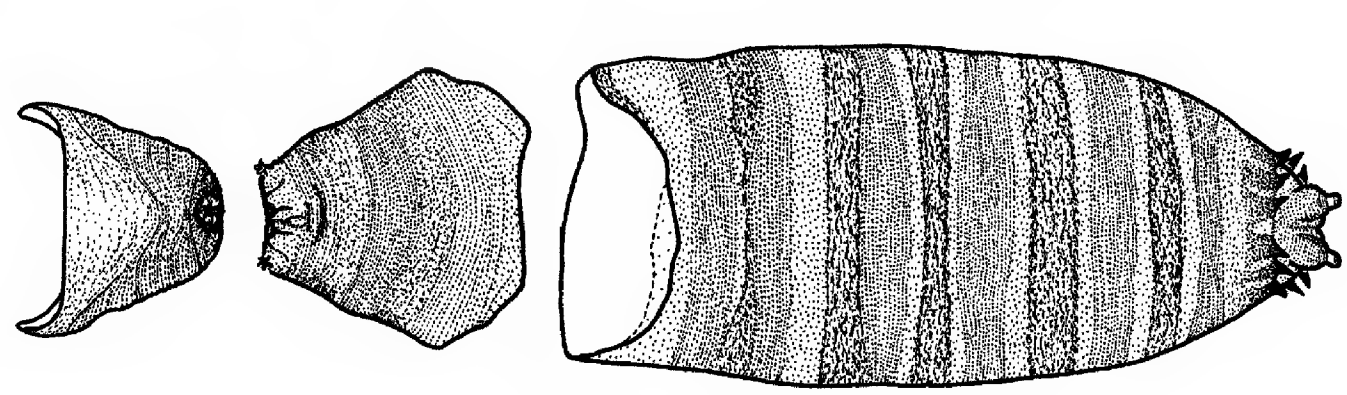
18 *Katacamilla*



19 *Katacamilla*



20 *Katacamilla*



21 *Katacamilla*

Figs 102.16–21. Immature stages of Camillidae: (16) prothoracic spiracle of *Katacamilla cavernicola* Papp, lateral view; (17) same, detail of abdominal creeping welt; (18) same, Keilin's organ on prothoracic segment; (19) same, posterior spiracle, caudal view; (20) same, cephaloskeleton, lateral view; (21) same, puparium, dorsal habitus. Figs 17, 18, 20, 21 (after Kirk-Spriggs *et al*. 2002, figs 15, 13, 12, 22, respectively), Figs 16, 19 (courtesy R. Meier).

Abbreviations: b scl – basal sclerite; d brg – dorsal bridge; d corn – dorsal cornu; den scl – dental sclerite; ecdys sc – ecdysial scar; int scl – intermediate sclerite; K org – Keilin's organ; mhk – mouthhook; pastm b – parastomal bar; pstig tft – peristigmatic tuft; spr op – spiracular opening; v corn – ventral cornu.

periodically, to splay beneath the folded wings. This results in a very marked and rhythmic up and down movement of the folded wings, and together with a similar movement of the abdominal apex may be part of a signalling repertoire during mating (Barraclough 1992).

Economic significance

Camillidae have no known economic significance.

Classification

The Camillidae belong to the superfamily Ephydroidea and until recently, were believed to have affinities only with the Curtonotidae, Ephydridae and Drosophilidae. Griffiths (1972: 102) considered them to be the sister-group of the Drosophilidae, McAlpine (1987: 1025) considered the Camillidae to be most closely related to the Curtonotidae and Drosophilidae, while Grimaldi (1990) considered Camillidae to be the sister-group of the Ephydridae. Pape *et al*. (2011) listed the Camillidae as one of seven families of the Ephydroidea, while notably Wiegmann *et al*. (2011) place the Camillidae as the sister-group to the Curtonotidae + Diastatidae. Conclusions from this last paper regarding acalyptrate relationships should, however, be treated with caution.

Two species of the fossil genus *Protocamilla* Hennig have been described from Baltic amber (one of these a remarkable stalk-eyed species (Grimaldi 2008)) and an additional three or four undescribed fossil species have also been recorded (Tschirnhaus & Hoffeins 2009).

No subfamily classification is currently recognised; *Katacamilla* is defined by a number of likely synapomorphies (Barraclough 1998*a*).

Identification

Aside from the adult family key provided in this *Manual* (see Chapter 12), southern African Camillidae can also be readily identified using the identification key of Barraclough (1995), which identifies most Southern African families of acalyptrate Diptera.

Most species of Camillidae are known from spot localities, although *Afrocamilla armata* (Hackman, 1960) is known from much of South Africa, as well as Kenya and Tanzania (Barraclough 1997*a*).

Afrocamilla are best identified using the identification key of Barraclough (1997*b*), although this only treats the South African species; four species-groups are recognised by Barraclough (1997*b*). Otherwise, recourse must be made to the original descriptions of *Afrocamilla*. Both *Teratocamilla* and the described species of *Camilla* Haliday can be identified in Barraclough (1993), although almost all Afrotropical species of *Camilla* from outside South Africa are probably undescribed. *Katacamilla* can be identified using the identification key of Barraclough (1998*a*). For studies of Camillidae of the Arabian Peninsula, reference should be made to the papers of Barraclough (1998*a*, 2004, 2005). All camillid genera, except *Teratocamilla*, have been recorded from the Arabian Peninsula.

There are a host of external morphological characters and also of the male and female postabdomen (including the spermathecae and ventral receptacle), that are useful for distinguishing and defining species and these cannot be fully enumerated here. Chaetotaxy and characters of the male terminalia (shape of epandrium, postgonite and epiphallus and shape and development of the distiphallus) are, however, especially important. *Katacamilla* species are somewhat difficult to identify and recourse must be made to the male terminalia and characters of the ctenidium on the fore femur. Camillidae are best micro-pinned in the field for later double-mounting (Nu-poly mounts) (see Chapter 2).

Key to genera of Afrotropical Camillidae

1. Antennal arista bare to pubescent (Fig. 5); thorax with 1 strong postsutural dorsocentral seta (Fig. 2); scutellar disc with small setulae; anepimeral seta differentiated; body mostly pallid in colour . . . . . *Katacamilla* Papp
– Antennal arista short to long plumose (e.g., Fig. 4); thorax with 2 strong postsutural dorsocentral setae; scutellar disc bare; anepimeral seta lacking; body brown, or frequently dark brown to black metallic in colour (e.g., Fig. 1) 2
2. Wing membrane entirely hyaline, without dark, transverse fascia near base of wing; abdomen without strikingly elongate, paired marginal setae on syntergite 1 + 2; posterior margin of syntergite 1 + 2 unmodified, not exserted above level of tergite 3; base of tergite 3 unmodified; body yellow-brown to brown, never dark brown to black and metallic . . . . . *Camilla* Haliday
– Wing membrane with variously developed dark basal transverse fascia (e.g., Fig. 6); abdomen with strikingly elongate, paired marginal setae on syntergite 1 + 2 (e.g., Fig. 8); posterior margin of syntergite 1 + 2 highly modified and exserted above level of tergite 3 (e.g., Figs 1, 8); base of tergite 3 invaginated beneath hind margin of syntergite 1 + 2; body often at least partly dark brown to black and metallic 3
3. Head without proclinate fronto-orbital seta; male tergite 5 unusually well-developed and elongate, undissected length subequal to or longer than that of tergite 4, forming prominent hood-like extension (Fig. 12) . . . . . *Teratocamilla* Barraclough
– Head often with proclinate fronto-orbital seta; male tergite 5 reduced, barely visible in undissected specimens . . . . . *Afrocamilla* Barraclough

Synopsis of the fauna

Camillidae comprises 38 species globally and is likely to be widespread throughout Africa and into the Arabian Peninsula. In the Afrotropics, however, it is currently only recorded from Ethiopia, Gambia, Kenya, Namibia, Oman, Nigeria, South Africa, Tanzania and Yemen. It is not yet recorded from Madagascar, or any of the Indian Ocean islands. There are currently 23 Afrotropical species of Camillidae; 12 Palaearctic species (one species introduced to North America); and four endemic species from the New World (Mexico and the United States of America).

***Afrocamilla* Barraclough.** This is the best known and most widespread genus in the Afrotropical Region, with published records from all the countries noted above, except Namibia and Nigeria. Currently, there are 13 described Afrotropical species. Three species have been described from the Nearctic Region by Barraclough & Wheeler (1995) and Barraclough & Fitzgerald (2001), one of which was collected from the droppings of the Bushy-tailed wood rat, *Neotoma cinerea* (Ord) (Cricetidae), all this suggesting a much wider distribution. Many additional species await description from the Afrotropical Region. The South African species were keyed by Barraclough (1997*b*).

***Camilla* Haliday.** A genus of 12, mainly Palaearctic species, also occurring in the Afrotropical, Nearctic and Neotropical Regions (Mexico). Only two species have been described from the Afrotropical Region, *C. capensis* Barraclough, 1993 and *C. manningi* Barraclough, 1993, both from South Africa, but additional unstudied material is available from Namibia (A.H. Kirk-Spriggs, pers. obs.) and an undescribed species has been examined from Kenya (Barraclough 1997*b*). It is likely that numerous additional species await discovery, including species from the Arabian Peninsula, with at least one undescribed species known from the United Arab Emirates. Little is known about the biology of *Camilla* in the Afrotropics, although the Kenyan species (noted above) was collected from hyrax droppings (Barraclough 1997*a*). Elsewhere, Basden (1961, cited in Papp 1998: 533), reared four of the five British species of *Camilla* from soil taken near the entrances of rabbit burrows. Basden also obtained the British species, *C. atrimana* Strobl, 1910, from the nest of a "small rodent (? shrew)" and there is material in his collection from the nest of the Common shrew, *Sorex araneus* L. (Soricidae), presumably representing the same record that Smith (1989: 106), following Collin (1933), attributed to the Short-tailed field vole, *Microtus agrestris* (L.) (Cricetidae). Smith (1989: 106) also noted that A.G. Irwin "… reared a species [of *Camilla*] from soil derived from feral pigeon guano". The specimen referred to is the British species, *C. glabra* (Fallén, 1823), which was reared from soil formed from feral pigeon guano at the base of a castle keep wall in Norfolk (A.G. Irwin and P. Chandler, pers comms. 2014). An identification key to the two described Afrotropical species is provided by Barraclough (1993).

***Katacamilla* Papp.** An endemic genus with one species also occurring in the Arabian Peninsula. There are currently six described Afrotropical species, which are recorded from Namibia, Nigeria, Oman, South Africa and Yemen and a new troglophilic species has been identified from Kenya (A.H. Kirk-Spriggs, pers. obs.). Given the troglophilic habit of some *Katacamilla* species, it is likely that several additional new species await discovery and further collecting efforts are strongly encouraged. An identification key to species was provided by Barraclough (1998).

***Teratocamilla* Barraclough.** An endemic monotypic genus, with the single species, *T. sineseta* Barraclough, 1993, described from the Eastern and Western Cape Provinces of South Africa. Nothing is known regarding the biology of the genus, although it is likely similar to that of *Afrocamilla*.

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CURTONOTIDAE 103

(Quasimodo Flies or Hunchbacked Flies)

Ashley H. Kirk-Spriggs

Fig. 103.1. Female of *Cyrtona* (*s.l.*) sp. (South Africa) (photograph © S.A. Marshall).

Diagnosis

Small- to medium-sized (body length: 2.2–12.0 mm), stout-bodied acalyptrate flies with hunchbacked appearance (Figs 1–5); colouration from pale straw yellow to dark brown, abdomen often maculate (Figs 1–5, 65–67, 86–90); wing hyaline, darkened over crossveins, infuscated or distinctly patterned, with cells *bm* and *dm* confluent (Figs 72–85).

Head (Figs 6–25), with compound eyes large and elliptical (Figs 6–8, 18–25), usually concolourous maroon with iridescent sheen in living flies (Figs 1–5); 3 ocelli present, on slightly raised ocellar triangle; frons flat (Figs 6, 7), or slightly convex (Fig. 8), usually with 2 interfrontal plates (Figs 6, 8–16, 18–24), except in *Tigrisomyia* Kirk-Spriggs (Figs 17, 25), with silvery margin adjacent to compound eye; frons usually wide in both sexes, but markedly narrower in males of *Axinota* Wulp (Kirk-Spriggs 2010*a*, figs 1–4); usually with 3 pairs of fronto-orbital setae; proclinate fronto-orbital seta usually strongly developed (Figs 6–10, 15) (greatly reduced or absent in *Axinota*, Fig. 9); posterior reclinate fronto-orbital seta always strongly developed (Figs 6–8, 10); anterior reclinate fronto-orbital seta greatly reduced, minute or microscopic (Figs 6–8); 1 pair of well-developed inner and outer vertical setae (Figs 6–8); ocellar setae strongly developed and divergent, equal in size to proclinate fronto-orbital setae (Figs 6–8); postocellar setae convergent or cruciate (Figs 6–17); occipital setae moderately well-developed, decreasing in size (Figs 6–8); gena relatively broad to narrow, with 1 vibrissa present and row of subvibrissal setae along genal suture (Figs 6–8); lunule narrow, indistinct and bare; face bare (Figs 6–8), usually with low facial carina (Fig. 7); oral margin concave; clypeus developed (Figs 6, 8); antenna (Figs 6–35) relatively small (Fig. 6), to large (Fig. 8); scape (Figs 26–35) small subtriangular, usually with a few setulae; pedicel (Figs 6–8, 26–35) larger, triangular or more globular, with distinct dorsolateral cleft (viewed from above) (Fig. 7), usually with 1 or 2 strong setae and setulae row along anterior margin; postpedicel (Figs 6–8, 26–35) largest antennomere, suspended

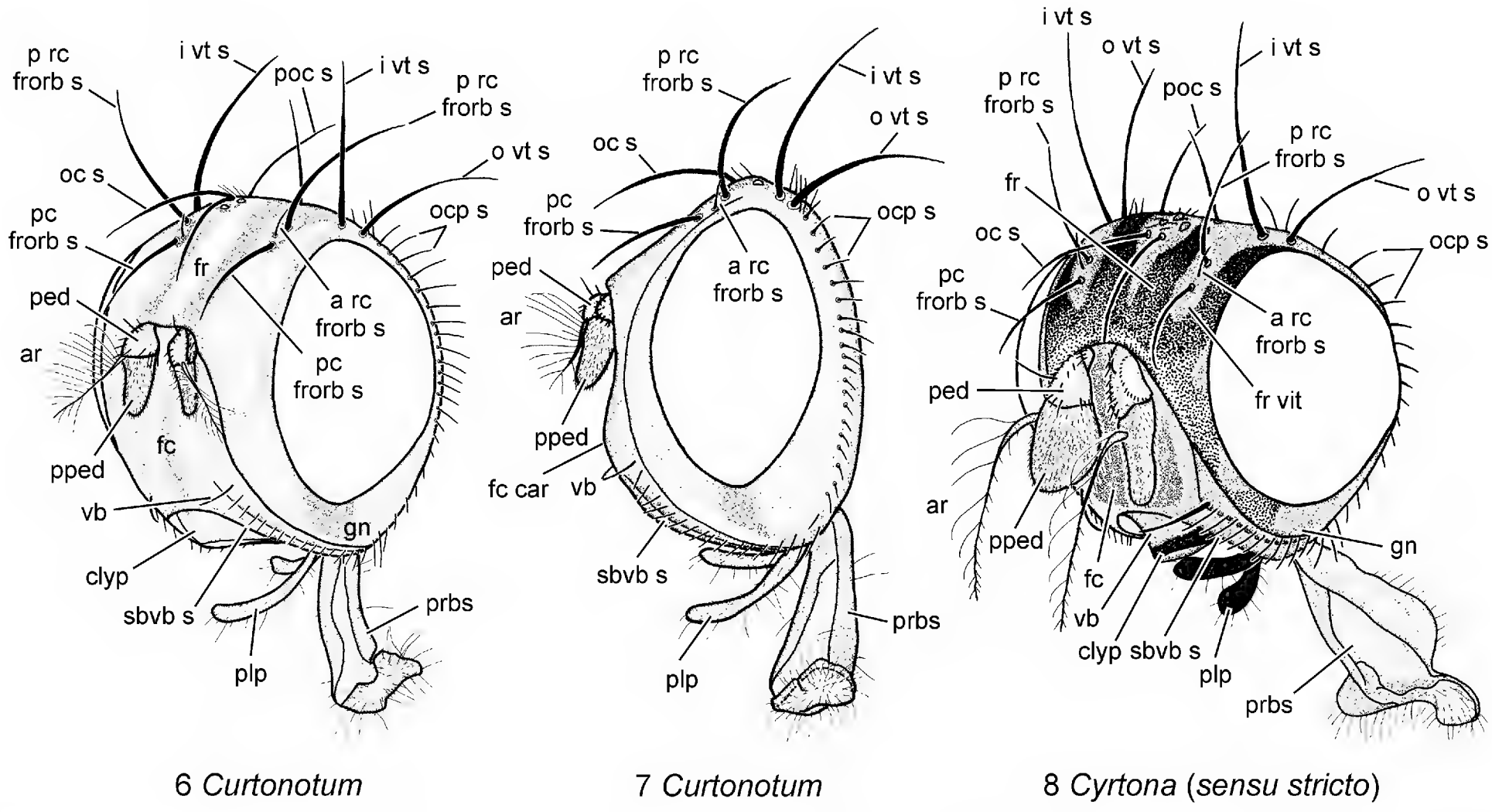
beneath pedicel, clothed in fine, close microtrichia, shape variable; arista (Figs 6–8, 26–35) invariably long and well-developed, with long dorsal and ventral microtrichia (Figs 6, 26, 28, 32–35), long dorsal and shorter ventral microtrichia (Figs 27, 30, 31), short dorsal and ventral microtrichia (Fig. 29), or short-pubescent (Undescribed genus C) (Fig. 24); palpus usually long and narrow, slightly spatulate and proboscis well-developed, with short setulae (Figs 6–8).

Thorax (Figs 1–5, 36–53, 65–71) with scutum distinctly domed (hunchbacked) in lateral view (Figs 1–5, 65–68), most extremely developed in *Axinota* (Figs 2, 45, 65, 68); scutum ground colour of varying colours and patterns, unicolourous or with mottled appearance, often with dorsocentral vittae (Figs 45, 46, 52), or these indistinct (Fig. 50) or absent (Undescribed genus B) (Fig. 51), *Tigrisomyia* with distinct maculae (Figs 5, 69–71); dorsum entirely clothed in close, irregularly arranged rows of short setae, sometimes with cuticle darkened around sockets (Figs 39, 47–49, 66); postpronotum distinct, with 2 or 3 postpronotal setae and smaller setulae (Figs 36–44); 1–2 pairs of large dorsocentral setae (Fig. 52); 1 pair acrostichal setae, same length as anterior dorsocentral seta (Fig. 52); presutural seta moderately strong, reclinate, weaker and shorter than posterior notopleural seta (Fig. 37); 2 notopleural setae of similar length (Fig. 37); 1 strong, reclinate supra-alar seta (Fig. 37); 1 strong reclinate postalar seta (Fig. 52); 1 strong intrapostalar seta (Fig. 52); anepisternum with 2–3 stronger anepisternal setae at posterior margin and moderately strong intermediate setae, with fine setulae scattered across surface (Figs 36–44); laterotergite and meron bare (Figs 36–44); katepisternum with 1–2 setae, if 2 then ventral seta stronger and dorsally directed, with fine setulae scattered across surface (Figs 36–44). Scutellum (Figs 45–64) with disk setulose (*Axinota*, Fig. 45; *Curtonotum* Macquart, Fig. 46; and Undescribed genus B, Fig. 51), or disk entirely bare (all other genera, Figs 47–50, 52, 53); with strong apical and basal scutellar setae (Fig. 50), often with smaller setae interspersed; subscutellum (Figs 54–64) well-developed and bulging to greater or lesser degree. Wing (Figs 72–85) with costal vein (C) either with large, conspicuous spines in basal ⅔ (*Curtonotum*, Fig. 74 and *Axinota fuscipennis* species-group, Fig. 72), or with short inconspicuous spines (*A. pictiventris* species-group and all other genera, Figs 73, 75–85); shape narrow to very broad, bluntly pointed or evenly rounded; membrane entirely hyaline (*A. pictiventris* species-group, Fig. 73), or largely infuscate (*A. fuscipennis* species-group, Fig. 72), brown or yellow without markings over crossveins (Figs 84, 85), pale grey or brown with darker markings over *r–m* and *dm–m* crossveins (Figs 74–76,

Figs 103.2–5. Photographs of living Curtonotidae: (2) *Axinota simulans* Delfinado (non-Afrotropical); (3) *Curtonotum uncinatum* species-group (Namibia); (4) *Cyrtona "Parapsinota"* sp. (Tanzania); (5) *Tigrisomyia amnoni* Kirk-Spriggs (Tanzania). Fig. 2 (photograph © C. Athul Sankar), Figs 3–5 (photographs © S.A. Marshall).

80, 81), with more diffuse darker markings (Figs 82, 83), or distinctly patterned (Figs 77–79); costal vein (*C*) with humeral and subcostal breaks (Fig. 74), subcostal vein (*Sc*) complete, reaching vein R_1 or merging with it (Fig. 74); costal vein (*C*) extending to vein R_{4+5} or slightly beyond (Figs 72–85); veins R_1, R_{2+3}, R_{4+5}, M_1 and M_4, all well-developed and reaching wing margin; vein *CuA+CuP* expressed as fold only, not reaching wing margin; vein A_1 expressed as a short stump only; vein R_1 short (Fig. 74); vein R_{2+3} usually straight or slightly curved (Fig. 74); vein R_{4+5} straight or slightly sinuous, ending at wing tip in all genera (Figs 72–85), with short auxiliary vein into cell *dm* in *Cyrtona* Séguy *sensu stricto* (Figs 77–79); vein M_1 parallel with vein R_{4+5} (Figs 75, 82–85), slightly converging apically (Figs 79, 80, 81, 85), or divergent (Figs 72, 73, 74); cells *bm* and *dm* confluent, forming cell *bm+dm* (Figs 72–85); cell *br* closed, cell *cua* closed (Fig. 74); crossvein *r–m* short, positioned at *ca* basal $^1/_5$ of wing length (Figs 72–85); crossvein *dm–m* longer and straight (Fig. 72), angled (Fig. 74) or sinuate (Fig. 77); anal lobe narrow (Figs 72, 85), broader and squarely angled (Fig. 74), or considerably broadened and rounded (Figs 77, 78, 84). Legs (Figs 1–5, 65, 66) normally rather pale to dark; all tibiae with strong pre-apical dorsal seta (Fig. 39); fore femur usually with row of 6 or 7 longer curved setae on anterior surface (Figs 37, 39); fore tibia with comb of very short, close-set spines (ctenidium) on anteroventral surface (Figs 36, 37) (probably serving grooming function).

Abdomen (Figs 1–5, 65–67, 86–90, 134, 135, 140–152), cylindrical and somewhat tapered at apex (Figs 86–90), setulose, with row of setae along posterior margin of tergites 2–5, entirely grey or maculate to greater or lesser degree; sternites 1–5 well-developed; spiracles 1–7 present, situated in membrane in both sexes; male abdomen with sternites 6 and 7 present, but narrow and slightly asymmetrical; tergites 6, 7 and 8 mostly membranous and atrophied in *Curtonotum*; male terminalia (Figs 91–133), with epandrium broadly saddle-shaped and setose, especially along apical margin and/or ventrolateral lobe (Figs 91, 93, 95, 98, 100, 103, 106, 109, 112, 114, 116, 118, 120, 122, 124, 126, 128, 130, 132); cerci with apices fused in some *Curtonotum*, extended into sclerotised process, clothed in medium to long setae (extremely long in *Tigrisomyia*, Fig. 132); surstylus variably developed from short, subtriangular (Fig. 95) to long and narrow (Fig. 103), bifurcate in *Axinota* (Figs 91, 93), spatulate on *Tigrisomyia* (Fig. 132) and greatly broadened and enlarged in Undescribed genus C (Fig. 130); hypandrium variable in shape, but formed of simple U-shaped structure; gonopod poorly defined and not visible in profile, usually formed of low blade, with one or more anterior setula(e); phallic complex C-shaped, usually large (Figs 92, 94, 96, 97, 99, 101, 102, 104, 105, 107, 108, 110, 111, 113, 115, 117, 119, 121, 123, 125, 129, 133), but reduced in Undescribed genus A and C (Figs 127, 131); phallapodeme Y-shaped, usually fully fused with basiphallus in *Axinota* and

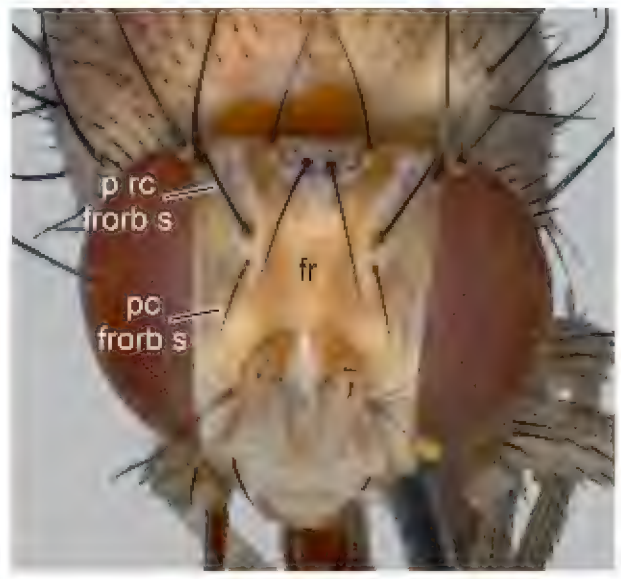


Figs 103.6–8. Heads of Curtonotidae (indicating major parts): (6) *Curtonotum herrero* Tsacas, oblique lateral view; (7) same, lateral view; (8) *Cyrtona* (*s.s.*) *pictipennis* (Thomson), oblique lateral view. Figs 6, 7 (Kirk-Spriggs & Wiegmann 2013, figs 154, 155 © Magnolia Press).

Abbreviations: a rc frorb s – anterior reclinate fronto-orbital seta; ar – arista; clyp – clypeus; fc – face; fc car – facial carina; fr – frons; fr vit – frontal vitta; gn – gena; i vt s – inner vertical seta; o vt s – outer vertical seta; oc s – ocellar seta; ocp s – occipital setae; p rc frorb s – posterior reclinate fronto-orbital seta; pc frorb s – proclinate fronto-orbital seta; ped – pedicel; plp – palpus; poc s – postocellar seta; pped – postpedicel; prbs – proboscis; sbvb s – subvibrissal seta; vb – vibrissa.

Curtonotum (e.g., Figs 92, 94, 99, 101, 104, 107, 110), but clearly separated in early branching *Curtonotum striatifrons* species-group (Fig. 96); basiphallus distinctly separate and connected to phallic plate in all other genera (Figs 113, 115, 117, 119, 121, 123, 125, 127, 129, 131, 133); ejaculatory apodeme on long external duct in most species (e.g., Figs 99, 113, 117, 123, 127, 129, 131, 133), but on very short duct in *Cu. striatifrons* species-group (Fig. 96), internal in *Axinota* (Figs 92, 94); distiphallus highly variable, divided in some genera, elongate or reduced, with inflatable sac in *Cyrtona "Parapsinota"* (Figs 123, 125); female abdomen (Figs 87, 88, 90, 134–152), tubular and telescopic in majority of (oviparous) species (e.g., Fig. 134), shorter and non-telescopic in larviparous species of *Cyrtona "Parapsinota"* (Fig. 135); tergites and

9 *Axinota*



10 *Curtonotum*

11 *Cyrtona* (*sensu lato*)

12 *Cyrtona* (*sensu stricto*)

13 *Cyrtona* "*Parapsinota*"

14 Undescribed genus A

15 Undescribed genus B

16 Undescribed genus C

17 *Tigrisomyia*

Figs 103.9–17. Heads of Curtonotidae (frontal views): (9) *Axinota quasimodoi* Kirk-Spriggs; (10) *Curtonotum uncinatum* Kirk-Spriggs; (11) *Cyrtona* (*s.l.*) *capensis* Hackman; (12) *Cy.* (*s.s.*) *pictipennis* (Thomson); (13) *Cy. "Parapsinota"* sp.; (14) Undescribed genus A; (15) Undescribed genus B; (16) Undescribed genus C; (17) *Tigrisomyia scoliosis* Kirk-Spriggs. Figs 9–17 (© Trustees of Natural History Museum, London).

Abbreviations: fr – frons; p rc frorb s – posterior reclinate fronto-orbital seta; pc frorb s – proclinate fronto-orbital seta.

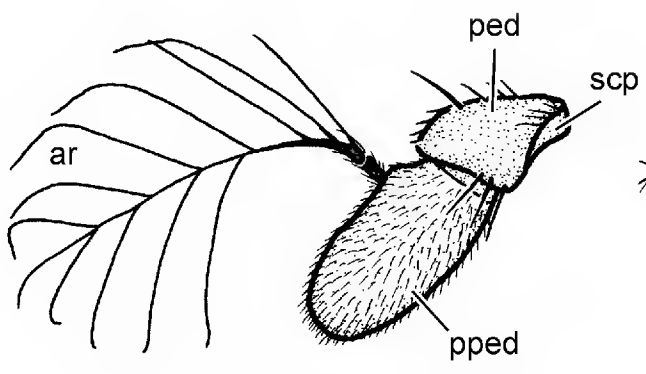
sternites 6–8 free and relatively unmodified, although sternite 8 reduced (Figs 140, 147–152); hypoproct triangular, sometimes partly or full divided (Figs 140, 147–152); epiproct and cercus fused in some *Curtonotum*, usually with long, fine setae (Figs 140, 147–152), or with short spines (in some extralimital *Curtonotum*); 2 spermathecae present (e.g., Figs 140, 141), variously shaped, from smooth globular and barrel-shaped to long, thin and studded with protuberances (Figs 153–168).

Egg (Figs 169–171), only known for non-Afrotropical *Cu. helvum* (Loew, 1862) (Meier *et al*. 1997), white and slender, length 0.98–1.13 mm, greatest width 0.26–0.32 mm; surface covered in longitudinal ridges lacking aeropyles (Fig. 170), with two ridges originating *via* bifurcation of single ridge; ridges flattened at anterior end, forming smooth cap from which micropyle arises (Fig. 169); micropyle in terminal position, consisting of single pore surrounded by chorionic welt (Fig. 169), forming cup-shaped structure; posterior end with ridges similarly fused, but posterior cap perforated by *ca* 100 aeropyles connected to underlying plastron (Fig. 171), each aeropyle surrounded by ring of thickened chorion, presumably strengthening edge of aeropyles; diameter of aeropyles smaller toward margin of posterior cap, with some located in furrows between chorionic ridges.

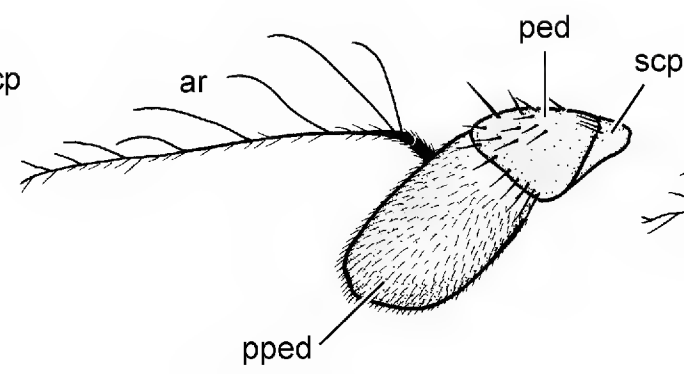
Larva (Figs 172–177), only described for the third-instar of *Cu. saheliense* (?) Tsacas, 1977 (Kirk-Spriggs 2008*b*), length 3.1 mm, width 0.85 mm at widest point; typical schizophoran, maggot-like, with 3 larval instars; respiratory system amphipneustic; colour dirty white, posterior spiracles darker reddish brown; shape cylindrical, anteriorly narrowed, bluntly pointed, posteriorly narrowed and truncate; thoracic segments with prothorax markedly shorter than mesothorax and this shorter than metathorax (Fig. 172); abdominal segments (Fig. 173) of approximately equal length, but segments 6 and 7 longer than 1–5, markedly so in segment 7, not bulging out medially and without processes of any kind; anal division sub-truncate, with ring of caudal tubules (Fig. 176); pseudocephalon (Figs 172, 175) inserted ventrally, retractile, anteriorly bilobed, approximately as long as wide, separated from prothorax by fleshy fold, with parallel rows of short, backwardly directed spinules, each cephalic lobe surrounding antenna glabrous (Fig. 175); cephalic lobes between maxillary palpus and mouth with extensive rows of overlapping cirri formed of relatively uniform

Figs 103.18–25. Heads of Curtonotidae (oblique lateral views): (18) *Curtonotum uncinatum* Kirk-Spriggs; (19) *Cyrtona* (*s.l.*) *capensis* Hackman; (20) *Cy.* (*s.s.*) *pictipennis* (Thomson); (21) *Cy. "Parapsinota"* sp.; (22) Undescribed genus A; (23) Undescribed genus B; (24) Undescribed genus C; (25) *Tigrisomyia scoliosis* Kirk-Spriggs. Figs 18–25 (© Trustees of Natural History Museum, London).

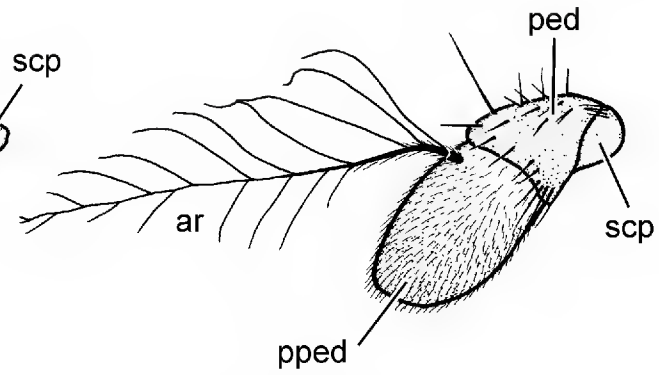
Abbreviations: ar – arista; fr – frons.



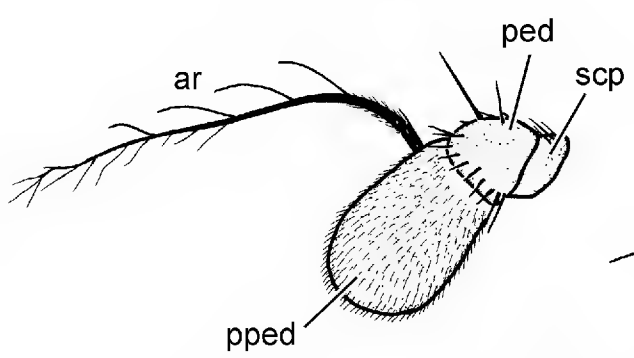
26 *Axinota*



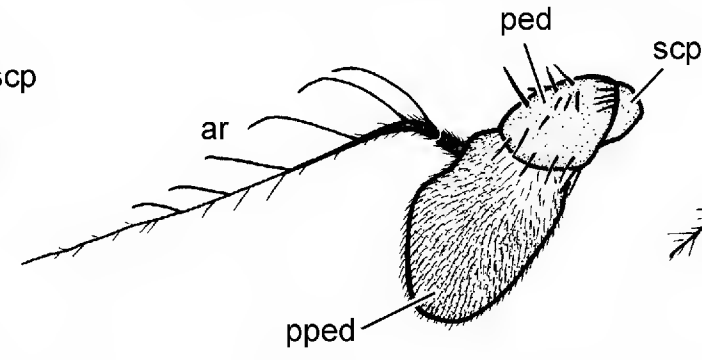
27 *Cyrtona* (*sensu stricto*)



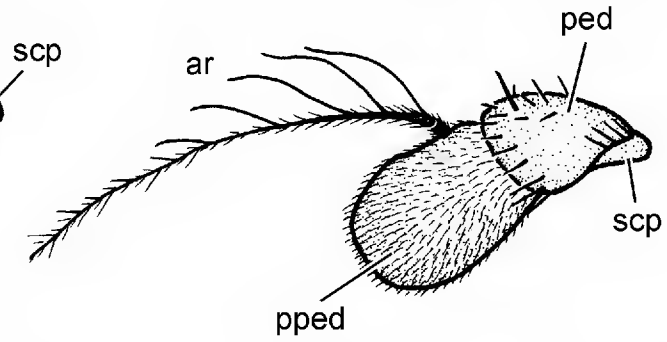
28 *Cyrtona* (*sensu stricto*)



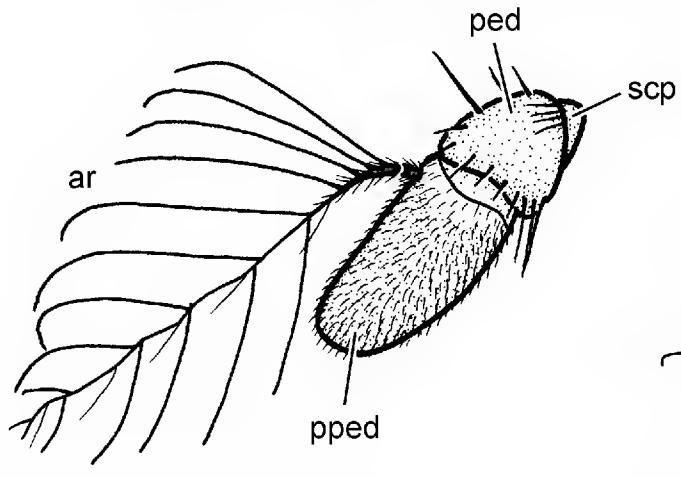
29 *Cyrtona* (*sensu stricto*)



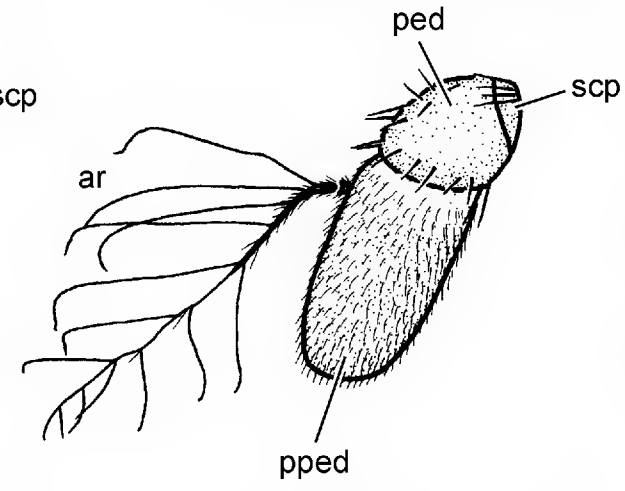
30 *Cyrtona* (*sensu lato*)



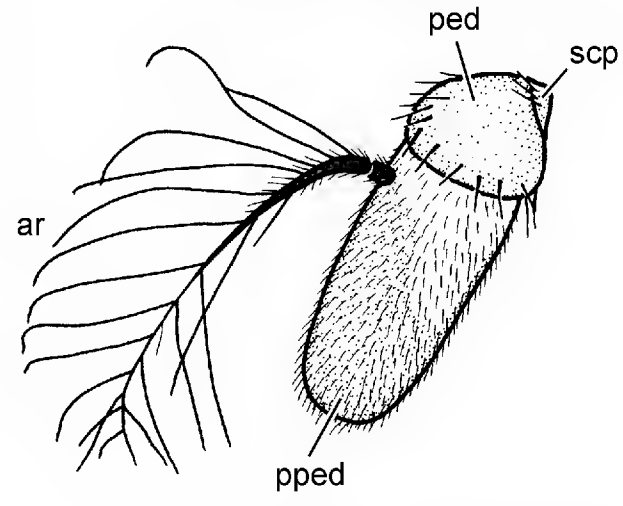
31 *Cyrtona* (*sensu lato*)



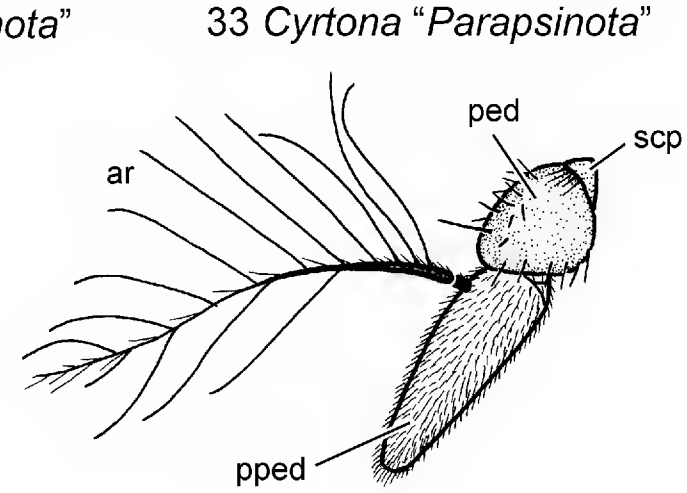
32 *Cyrtona* "*Parapsinota*"



33 *Cyrtona* "*Parapsinota*"



34 Undescribed genus A

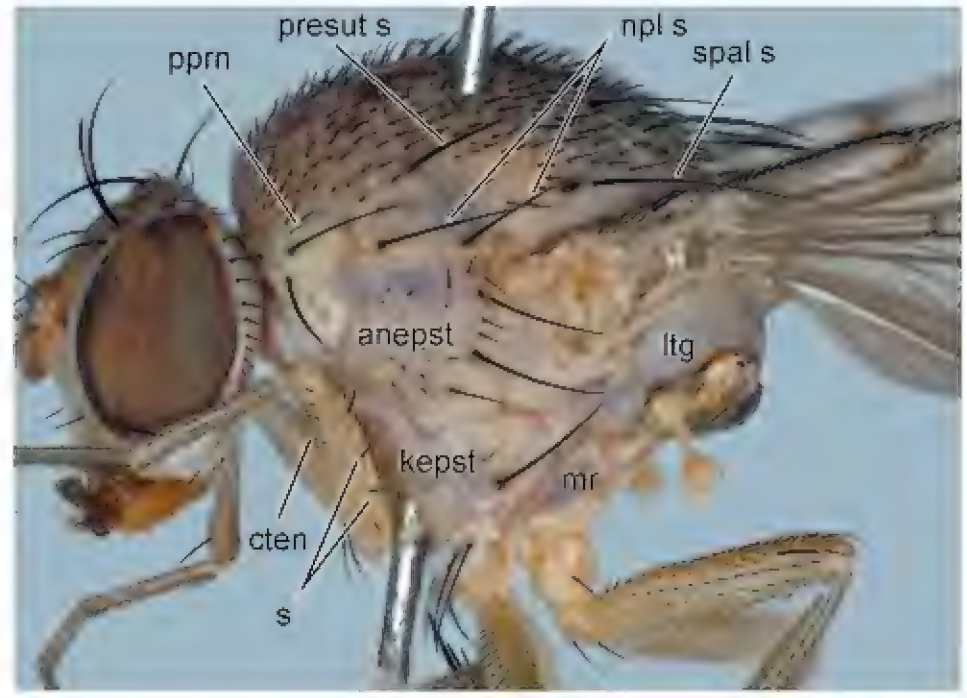


35 *Tigrisomyia*

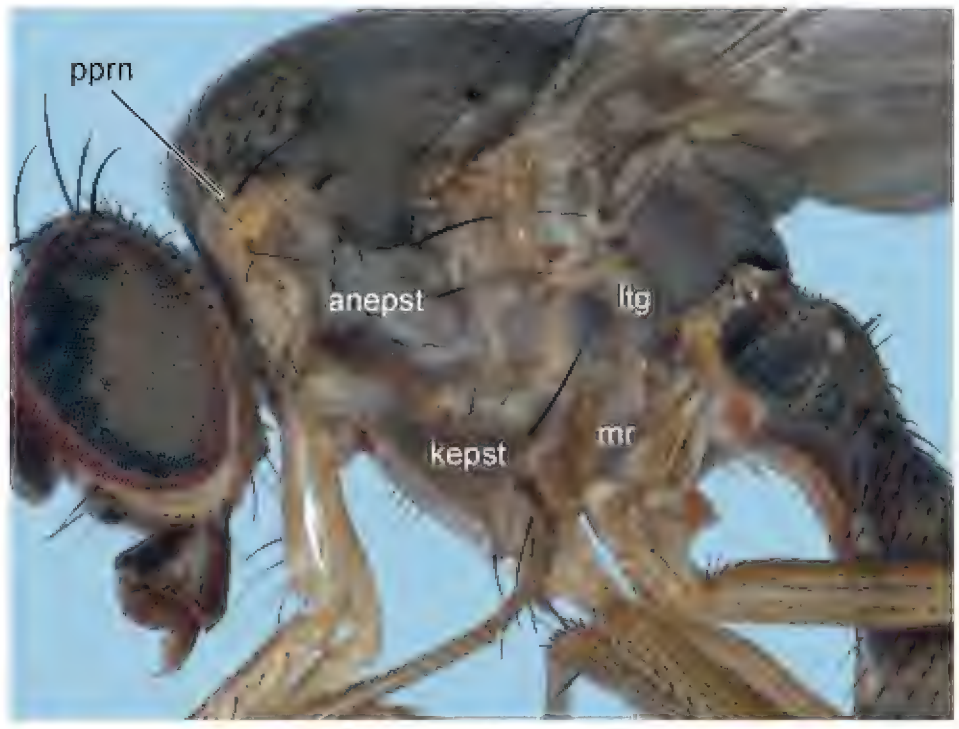
Figs 103.26–35. Antennae of Curtonotidae (lateral views): (26) *Axinota quasimodoi* Kirk-Spriggs; (27) *Cyrtona* (*s.s.*) *pictipennis* (Thomson); (28) *Cy.* (*s.s.*) *appendiculata* Séguy; (29) *Cyrtona* (*s.s.*) sp.; (30) *Cy.* (*s.l.*) *capensis* Hackman; (31) *Cy.* (*s.l.*) *consobrina* Hackman; (32) *Cy. "Parapsinota" albomacula* (Curran); (33) *Cy. "Parapsinota" sublineata* Duda; (34) Undescribed genus A; (35) *Tigrisomyia amnoni* Kirk-Spriggs. Figs 26–35 (Kirk-Spriggs & Wiegmann 2013, figs 27, 29, 30, 32, 33–36, 32, 28, respectively © Magnolia Press).

Abbreviations: ar – arista; ped – pedicel; pped – postpedicel; scp – scape.

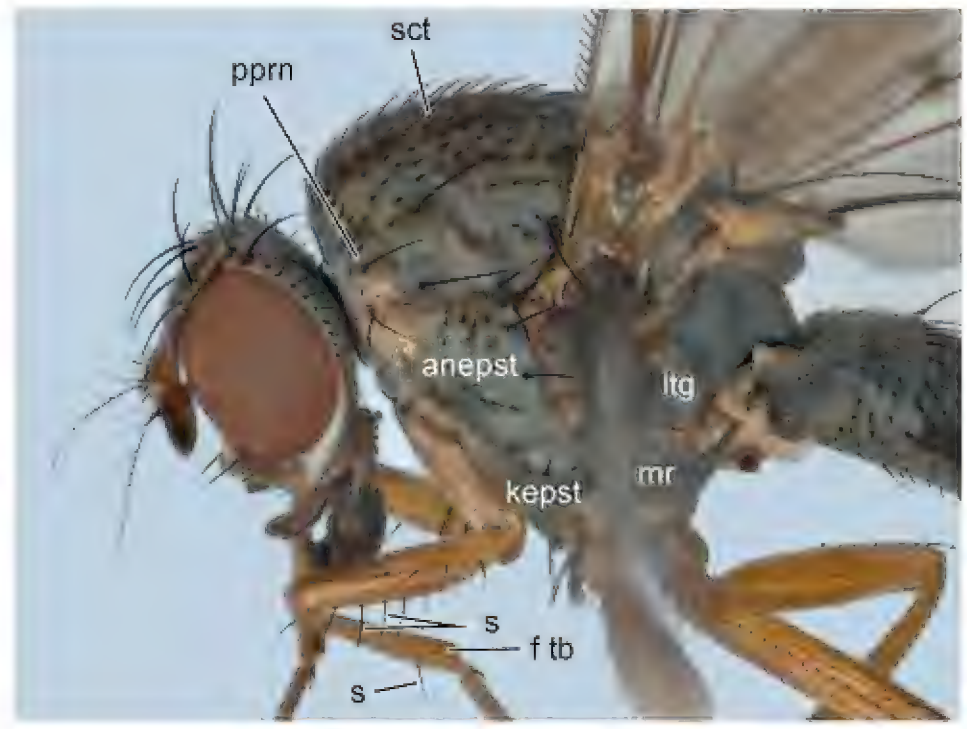
36 *Axinota*



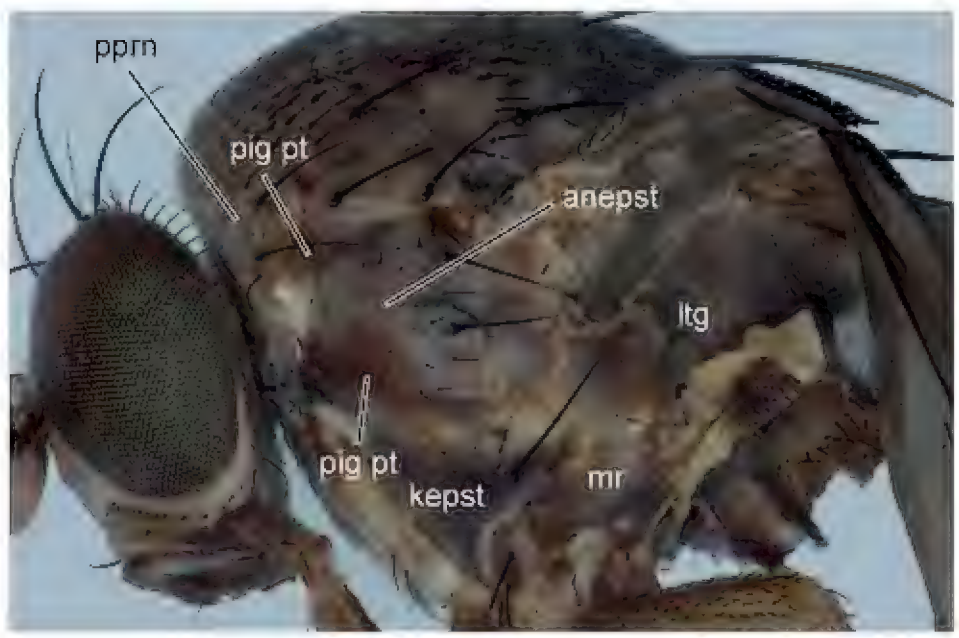
37 *Curtonotum*



38 *Cyrtona* (*sensu lato*)



39 *Cyrtona* (*sensu stricto*)



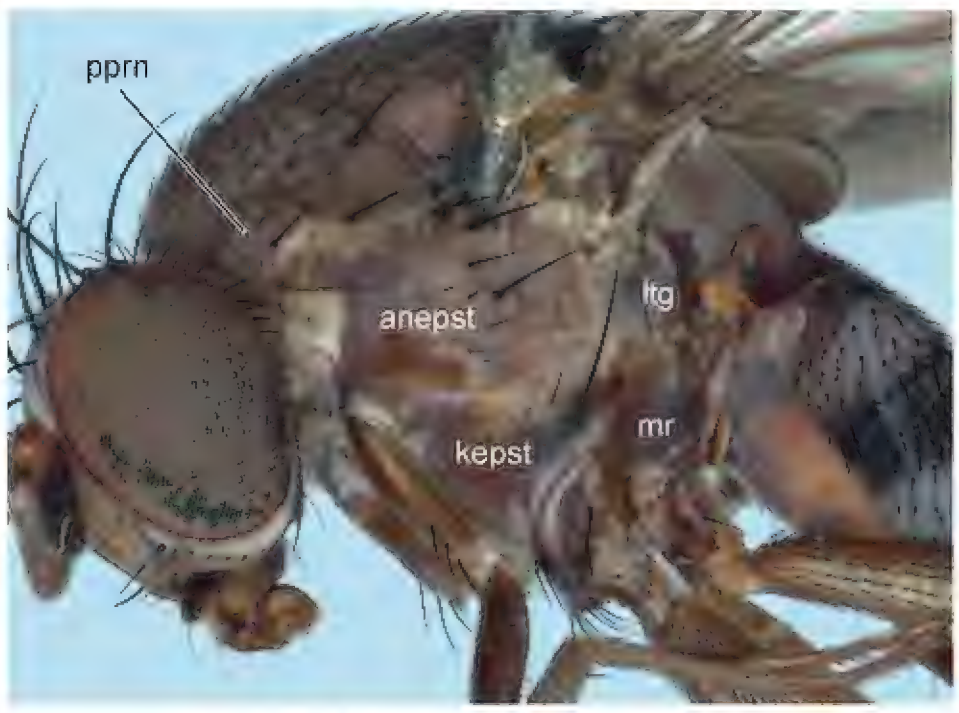
40 *Cyrtona* "*Parapsinota*"

41 Undescribed genus A

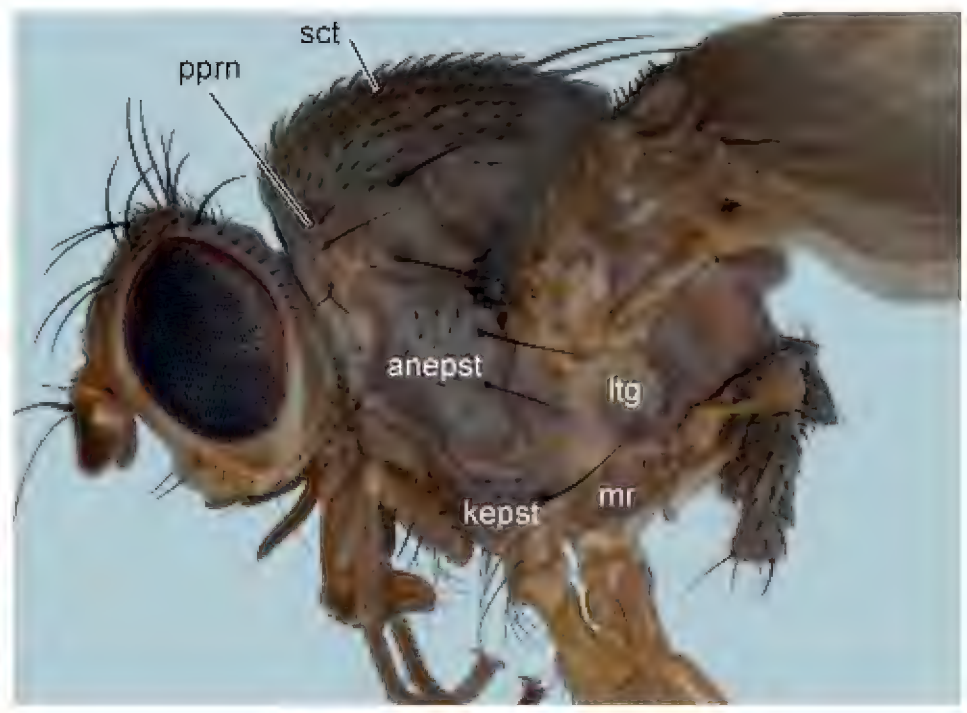
Figs 103.36–41. Thoraces of Curtonotidae (lateral views): (36) *Axinota quasimodoi* Kirk-Spriggs; (37) *Curtonotum cuthbertsoni* Duda; (38) *Cyrtona* (*s.l.*) *capensis* Hackman; (39) *Cy.* (*s.s.*) *pictipennis* (Thomson); (40) *Cy. "Parapsinota"* sp.; (41) Undescribed genus A. Figs 36–41 (© Trustees of Natural History Museum, London).

Abbreviations: anepst – anepisternum; cten – ctenidium; f tb – fore tibia; kepst – katepisternum; ltg – laterotergite; mr – meron; npl s – notopleural seta; pig pt – pigmentation patch; pprn – postpronotum; presut s – presutural seta; s – seta(e); sct – scutum; spal s – supra-alar seta.

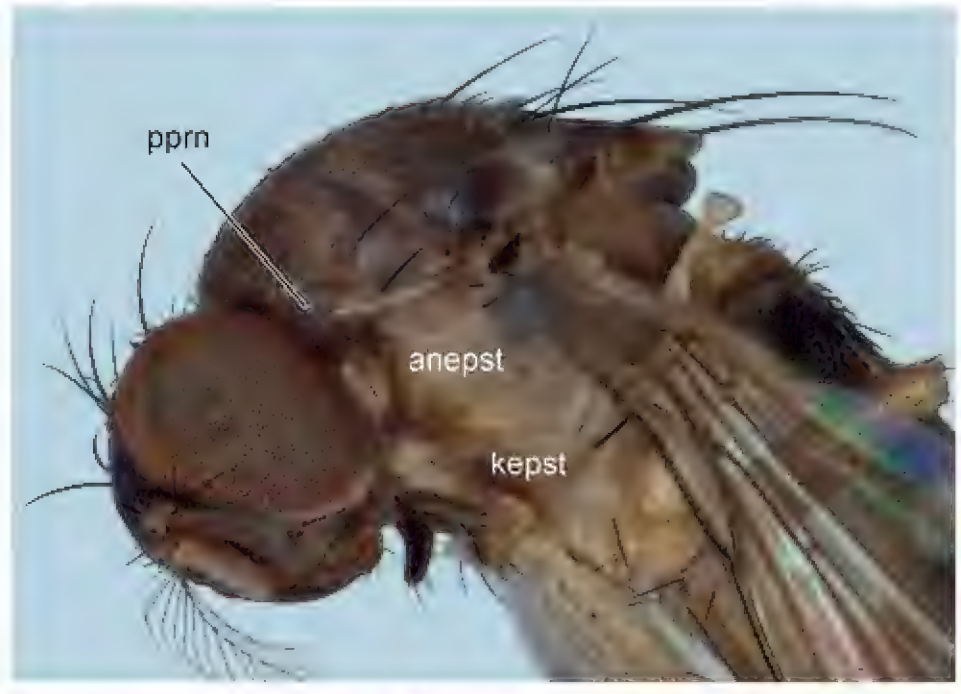
abutting rows, those adjacent to maxillary palpus with fringe of flattened, uniform, sharp digitations, those nearer mouth less compacted and down-curved; antenna (Fig. 175) apparently 2-segmented, relatively large, in terminal position, composed of elongated distal dome inserted into indistinct basal ring; maxillary palpus (Fig. 175), ventrolateral to antenna, with sensillae arranged collectively in ring and surrounded by 4 elongated fleshy folds; 2 antennal sensillae partially separated from 3 maxillary palpus sensillae; prothoracic spiracle (Fig. 174) fan-shaped with molar tooth-shaped short papillae (exact number undetermined), on broad, laterally expanded lobe-like projection; creeping welts on thoracic segments on anterior ½ or more of segment (Fig. 172), arranged as inverted V-shape laterally, encircling body segments, apparently as equally pronounced dorsally, ventrally and laterally; prothorax and mesothorax studded with short, closely packed, blunt spinules loosely arranged in multiple rows, single or bifurcated; abdomen (Fig. 173) with welts homogenous, comprising single short, bluntly pointed, backwardly directed spinules, arranged in regular to irregular rows; cuticle between welts glabrous laterally, formed of half moon-shaped crescents, sometimes partly studded with low, less conspicuous spinules; anal division (Fig. 176) with sharp irregular spinules throughout, except in vicinity of posterior spiracle; defined paired protuberances surrounding posterior spiracle in ring; posterior spiracles (Fig. 177), on defined, but short projections of anal division, each with 3 radial slit-like spiracular openings, surface between them glabrous, positioned on irregularly rounded spiracular plate; ecdysial scar large, oval and conspicuous; with 4 peristigmatic tufts, originating adjacent to spiracular openings on spiracular plate, filaments relatively short and flattened, some branched, not extending beyond spiracular plate, each spiracle surrounded by raised fleshy folded area (Fig. 176). Cephaloskeleton (Figs 181, 182), with mouthhooks jet-black, scimitar-shaped, relatively narrow, with single blunt accessory tooth, ventral surface beyond slightly irregular, not exhibiting row of regular distinct teeth (as



42 Undescribed genus B



43 Undescribed genus C



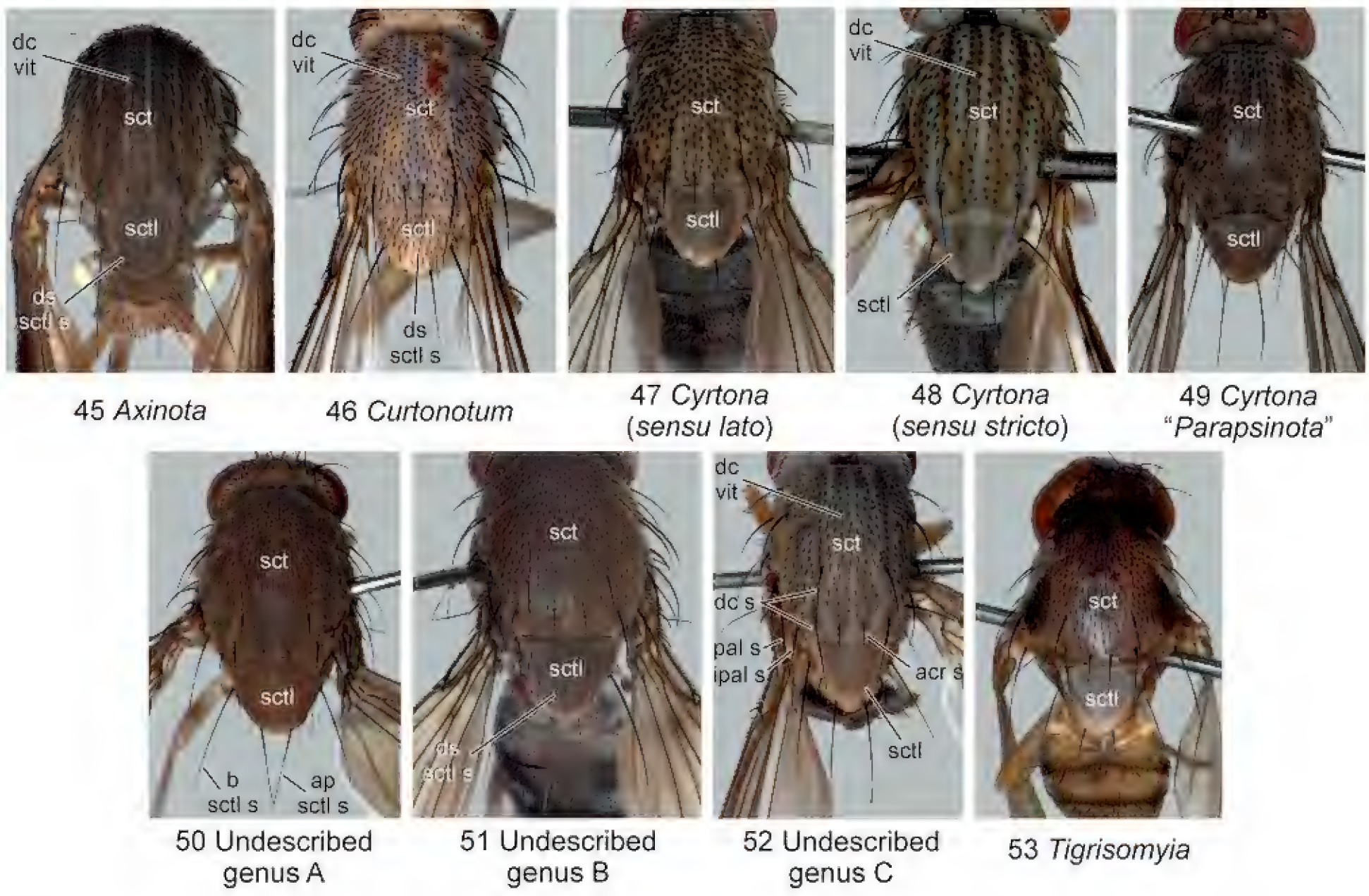
44 *Tigrisomyia*

Figs 103.42–44. Thoraces of Curtonotidae (lateral views): (42) Undescribed genus B; (43) Undescribed genus C; (44) *Tigrisomyia scoliosis* Kirk-Spriggs. Figs 42–44 (© Trustees of Natural History Museum, London).

Abbreviations: anepst – anepisternum; kepst – katepisternum; ltg – laterotergite; mr – meron; pprn – postpronotum; sct – scutum.

illustrated by Greathead 1958) (Fig. 181), campaniform sensillum not visible as tiny window, posteriorly angulate (in profile), indented, with posterior upper corner backwardly expanded, closely adjoining intermediate sclerite; dental sclerite deep black in colour, indistinctly comma-shaped and carrying adductor apodemes to mouthhooks, extending beneath mouthhooks in region of accessory tooth; intermediate sclerite black-brown apically and ventrally, brownish in dorsolateral region, deep black, H-shaped (viewed from above), short and broad, as long as wide; basal sclerite V-shaped, dorsal cornu pointed, with strongly developed V-shaped extension of cuticle basally, brown-black throughout, except in apical region, ventral cornu sub-truncate, with developed elongated lobe, predominantly yellow-brown, except inner margin brown-black, closed windows and cuticular sieves not evident.

Puparium (Figs 178–180) only described for *Cu. saheliense*, *Cu. simile* Tsacas, 1977 (Greathead 1958, as *Cyrtonotum cuthbertsoni*; Kirk-Spriggs 2008*b*) and non-Afrotropical *Cu. helvum* (Meier *et al*. 1997), length of puparial trunk (minus puparial caps): 4.5 mm; width at widest point: 2.0 mm; shape (Fig. 178) cylindrical, very slightly dorsoventrally flattened, relatively convex, acutely curved at sides, widest at abdominal segment 4; devoid of protuberances on abdominal segments 1–7; abdominal segment 6 and 7 longer than 1–5, markedly so in segment 7; thoracic segments chestnut brown, matt, darker than abdominal segments 1–7, prothoracic spiracle jet-black and shiny throughout and surrounding base; abdominal segments 1–7 uniform chestnut brown, cuticle thin and translucent, slightly darker at segmental borders, surface shiny, matt in area of creeping welts; creeping welts and anal division darker, chestnut brown, rugose throughout, subshiny; ring of caudal tubules (Fig. 180) dark reddish brown apically and basally; posterior spiracle deep reddish black, anal pad contrasting matt, chestnut brown, especially at its borders; creeping welts at anterior margin of segmental borders, encircling puparium, but less apparent dorsally, laterally developed as slightly impressed pads, spinules arranged in slightly crescent-shaped, overlapping, transverse, sinuous rows of saw-like, flattened, bluntly pointed spinules, some bifurcate, surface between these microscopically folded in transverse lines; prothoracic spiracles with 6 short spiracular papillae

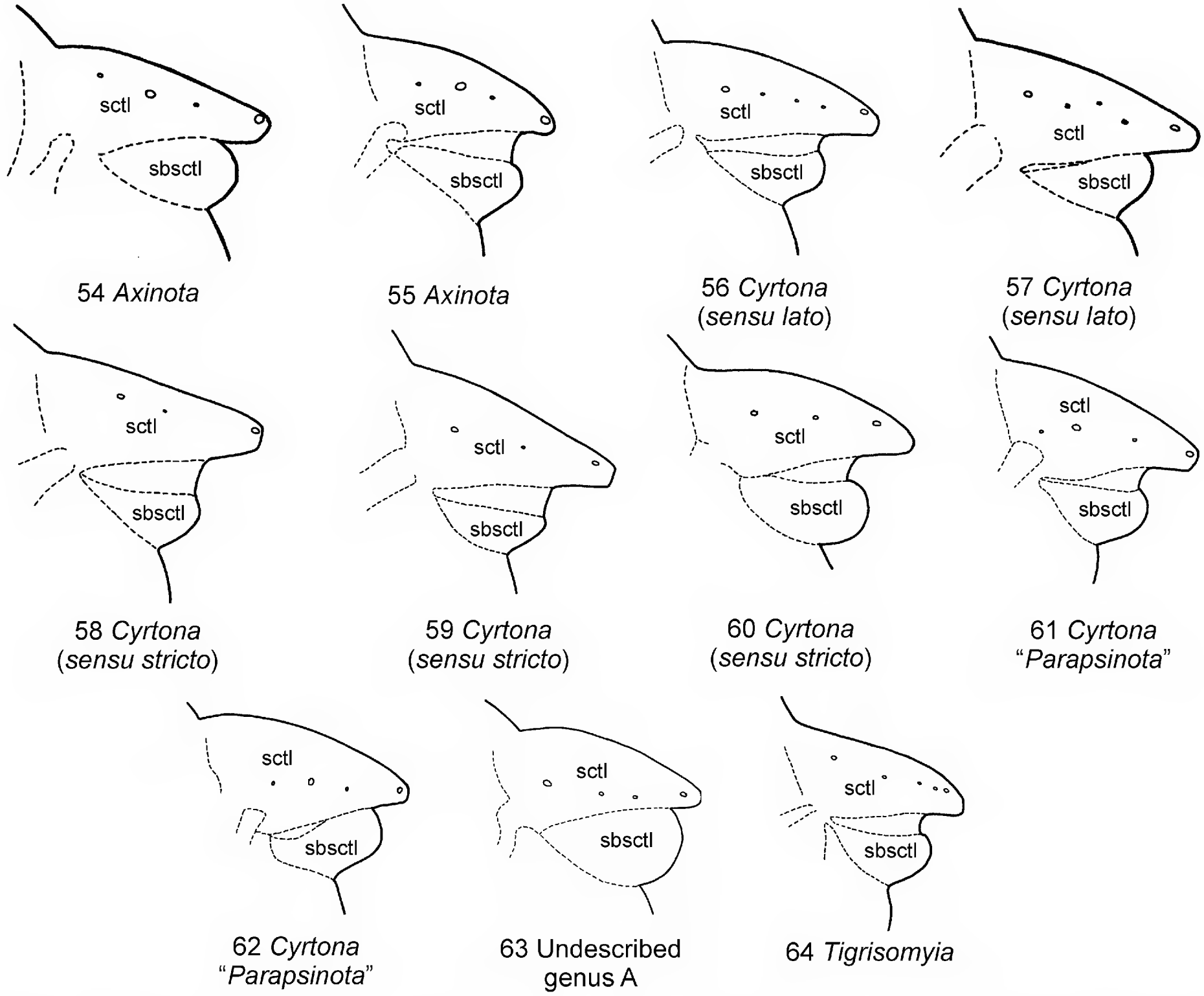


Figs 103.45–53. Thoraces of Curtonotidae (dorsal views): (45) *Axinota quasimodoi* Kirk-Spriggs; (46) *Curtonotum cuthbertsoni* Duda; (47) *Cyrtona* (*s.l.*) *capensis* Hackman; (48) *Cy.* (*s.s.*) *pictipennis* (Thomson); (49) *Cy. "Parapsinota"* sp.; (50) Undescribed genus A; (51) Undescribed genus B; (52) Undescribed genus C; (53) *Tigrisomyia scoliosis* Kirk-Spriggs. Figs 45–53 (© Trustees of Natural History Museum, London).

Abbreviations: acr s – acrostichal seta; ap sctl s – apical scutellar seta; b sctl s – basal scutellar seta; dc s – dorsocentral setae; dc vit – dorsocentral vitta; ds sctl s – discal scutellar seta; ipal s – intrapostalar seta; pal s – postalar seta; sct – scutum; sctl – scutellum.

on expanded fleshy base, these apically sub-divided, with slit-like spiracular openings; anal division with entire surface folded, forming regular to irregular lines, with 7 paired caudal tubules and single anal tuft surrounding caudal end, anal pad laterally expanded, with cuticle to either side of anal opening expanded into 2 broad semicircular areas, anal opening slit-like; posterior spiracles (Fig. 180) on slightly raised spiracular plate, margins very slightly shamrock-shaped, not entirely rounded (as in *Cu. helvum*), with 3 radial spiracular openings, conspicuous rounded ecdysial scar and 4 short, flattened peristigmatic tufts that do not extend beyond margin of spiracular plate.

Adult Curtonotidae are often confused with Drosophilidae (see Chapter 106), sharing a similar arrangement of fronto-orbital setae and being similar in genera appearance, but Curtonotidae are mainly distinguished by the distinctly setose anepisternum (Figs 36–44). Anepisternal setae are absent in all Drosophilidae (except four Oriental and Australasian species: *Mycodrosophila heterothrix* McEvey & Bock, 1981, *Scaptodrosophila merdae* (Bock, 1984), *S. paraguma* (Okada & Carson, 1980) and *Zaprionus obscuricornis* (de Meijere, 1916) (Kirk-Spriggs & Wiegmann 2013). Curtonotidae are also sometimes confused with Diastatidae (see Chapter 104), but Diastatidae have a characteristic arrangement of fronto-orbital setae, with the reclinate fronto-orbital setae inserted below the insertion of the proclinate fronto-orbital seta and Curtonotidae have the *bm* and *dm* wing cells confluent (without a *bm–m* crossvein) (Figs 72–85), but crossvein *bm–m* is present in Diastatidae (or partially so in *Campichoeta* Macquart).



Figs 103.54–64. Scutella of Curtonotidae (lateral views): (54) *Axinota quasimodoi* Kirk-Spriggs; (55) *Axinota* sp. (non-Afrotropical); (56) *Cyrtona* (*s.l.*) *capensis* Hackman; (57) *Cy.* (*s.l.*) *consobrina* Hackman; (58) *Cy.* (*s.s.*) *appendiculata* Séguy; (59) *Cy.* (*s.s.*) *pictipennis* (Thomson); (60) *Cyrtona* (*s.s.*) sp.; (61) *Cy. "Parapsinota" albomacula* (Curran); (62) *Cy. "Parapsinota" sublineata* Duda; (63) Undescribed genus A; (64) *Tigrisomyia amnoni* Kirk-Spriggs.

Abbreviations: sbsctl – subscutellum; sctl – scutellum.

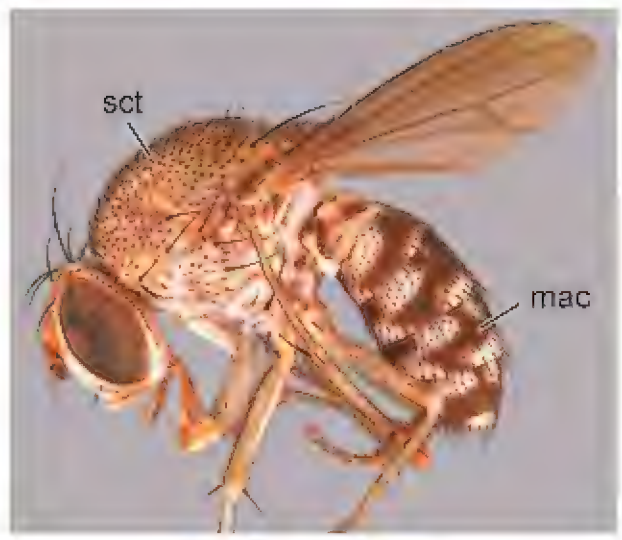
Biology and immature stages

The biology and immature stages of most Curtonotidae other than some *Curtonotum* species remain poorly known. The biology, larval habits and immature stages of other genera remain entirely unknown, although at least some undescribed species of *Cyrtona "Parapsinota"* are known to be viviparous (Pollock 1996) (Figs 135–139). What is known regarding the biology and behaviour of the genus *Curtonotum* (specifically) has been summarised by Meier *et al*. (1997), Tsacas (1977) and more recently by Kirk-Spriggs (2008*a*: 704, *b*, 2011), Kirk-Spriggs & Freidberg (2007), Kirk-Spriggs & Wiegmann (2013), Klymko & Marshall (2011) and Marshall *et al*. (2010: 1189).

Cuthbertson (1936) was the first to record the habit of daylight roosting in Aardvark, *Orycteropus afer* (Pallas) (Orycteropidae) and Warthog, *Phacochoerus aethiopicus* (Pallas) (Suidae), burrows in the Afrotropics, noting this behaviour in *Cu. quinquevittatum* Curran, 1933 (as *quinquevittata*) and *Cu. cuthbertsoni* Duda, 1935, in Zimbabwe. He suggested (p. 54), that the latter species: "Probably breeds in the faeces of these burrowing animals." Roosting behaviour was further noted by Tsacas (1977) for *Cu. sao* Tsacas, 1977 (actually in company with *Cu. saheliense*), in the burrow of Porcupine, *Atherurus africanus* Gray (Hystricidae), in Nigeria, and for *Cu. maculiventris* (Enderlein, 1917) (as *Cu. tigrinum* Séguy) in Warthog burrows in Kruger National Park, South Africa. In a study conducted in Zimbabwe, Pollock (2002) noted that during the dry season *Cu. quinquevittatum* rests by day in burrows of Warthog and Aardvark, but also in other natural and artificial holes, such as culverts. He noted that the greatest numbers of flies were found in recently vacated Warthog burrows, where flies occurred in their hundreds. He recorded that flies vacate these burrows about half an hour before sunset and return in the early morning, about sunrise. Dissected flies revealed a full crop of clear liquid, suggesting that this may be nectar and that flies may spend the night visiting flowers.

In a study conducted during the hot-dry season in the Zambezi Region of Namibia, the writer sampled adults from used and disused Aardvark burrows in the Mesic Savanna Biome. *Curtonotum bicuspis* Kirk-Spriggs, 2013, *Cu. uncinatum*

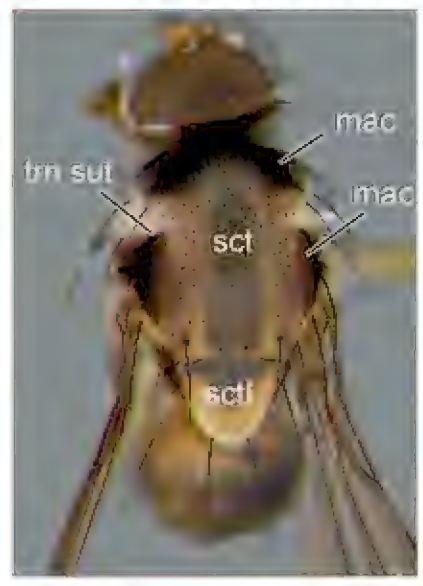
65 *Axinota*



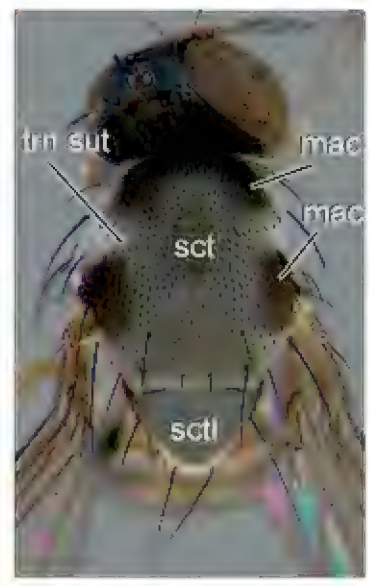
66 *Curtonotum*

67 *Curtonotum*

68 *Axinota*



69 *Tigrisomyia*

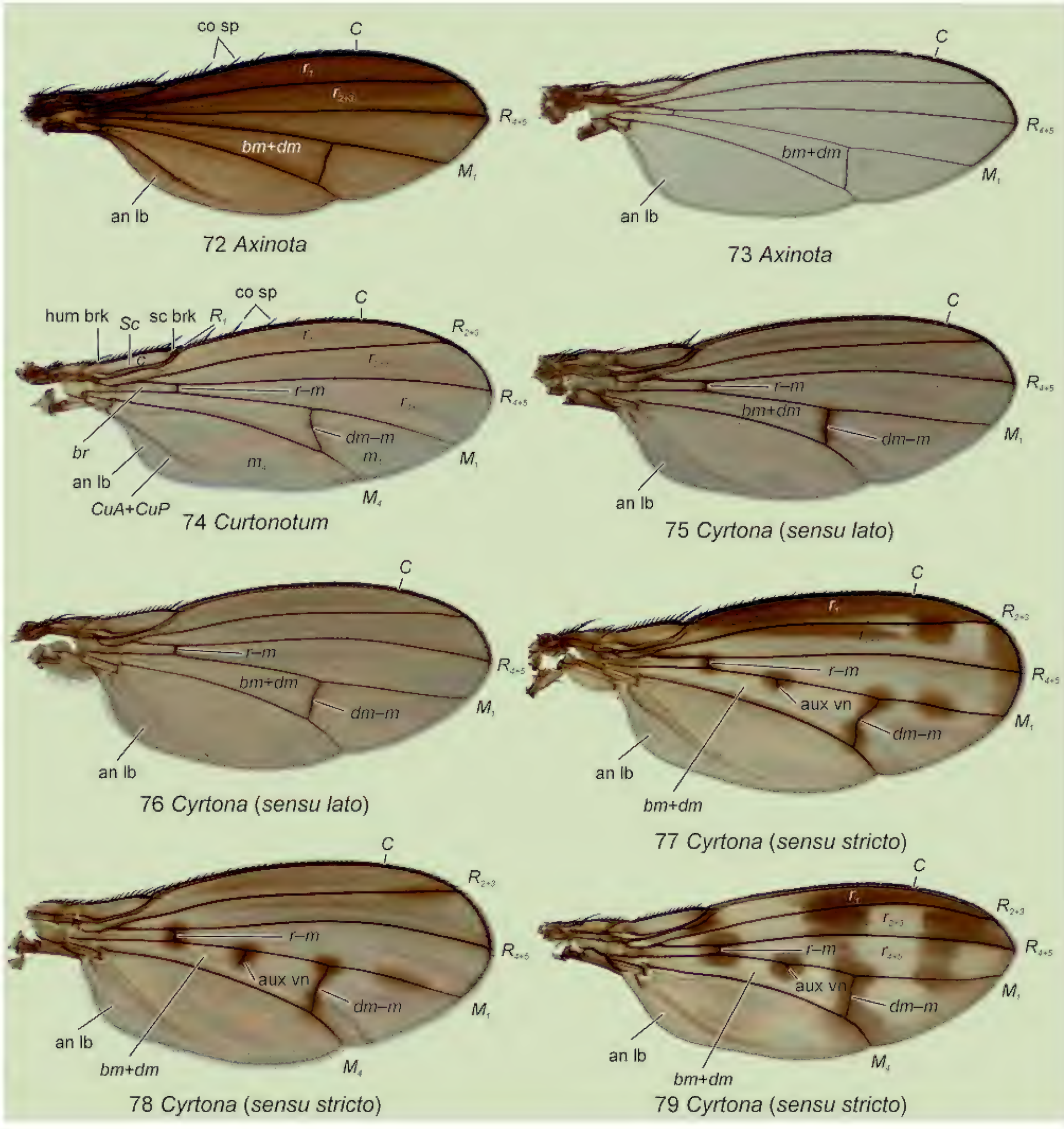


70 *Tigrisomyia*

71 *Tigrisomyia*

Figs 103.65–71. Habitus and heads and thoraces of Curtonotidae: (65) habitus of *Axinota fuscipennis* (Macquart), lateral view ♀; (66) same, *Curtonotum sternithrix* Tsacas, lateral view ♂; (67) same, *Cu. maculiventris* (Enderlein) ♂; (68) head and thorax of *A. quasimodoi* Kirk-Spriggs, frontolateral view ♂; (69) head and thorax of *Tigrisomyia kinskii* Kirk-Spriggs, dorsal view ♂; (70) same, *T. rhayaderi* Kirk-Spriggs ♀; (71) same, lateral view. Fig. 65 (after Kirk-Spriggs 2010*a*, fig. 31), Fig. 67 (after Kirk-Spriggs & Wiegmann 2013, fig. 107 © Magnolia Press), Fig. 68 (© Trustees of Natural History Museum, London), Figs 69–71 (after Kirk-Spriggs 2010*b*, figs 17, 15, 19, respectively).

Abbreviations: dc vit – dorsocentral vitta; mac – macula; sct – scutum; sctl – scutellum; trn sut – transverse suture; sct – scutum.



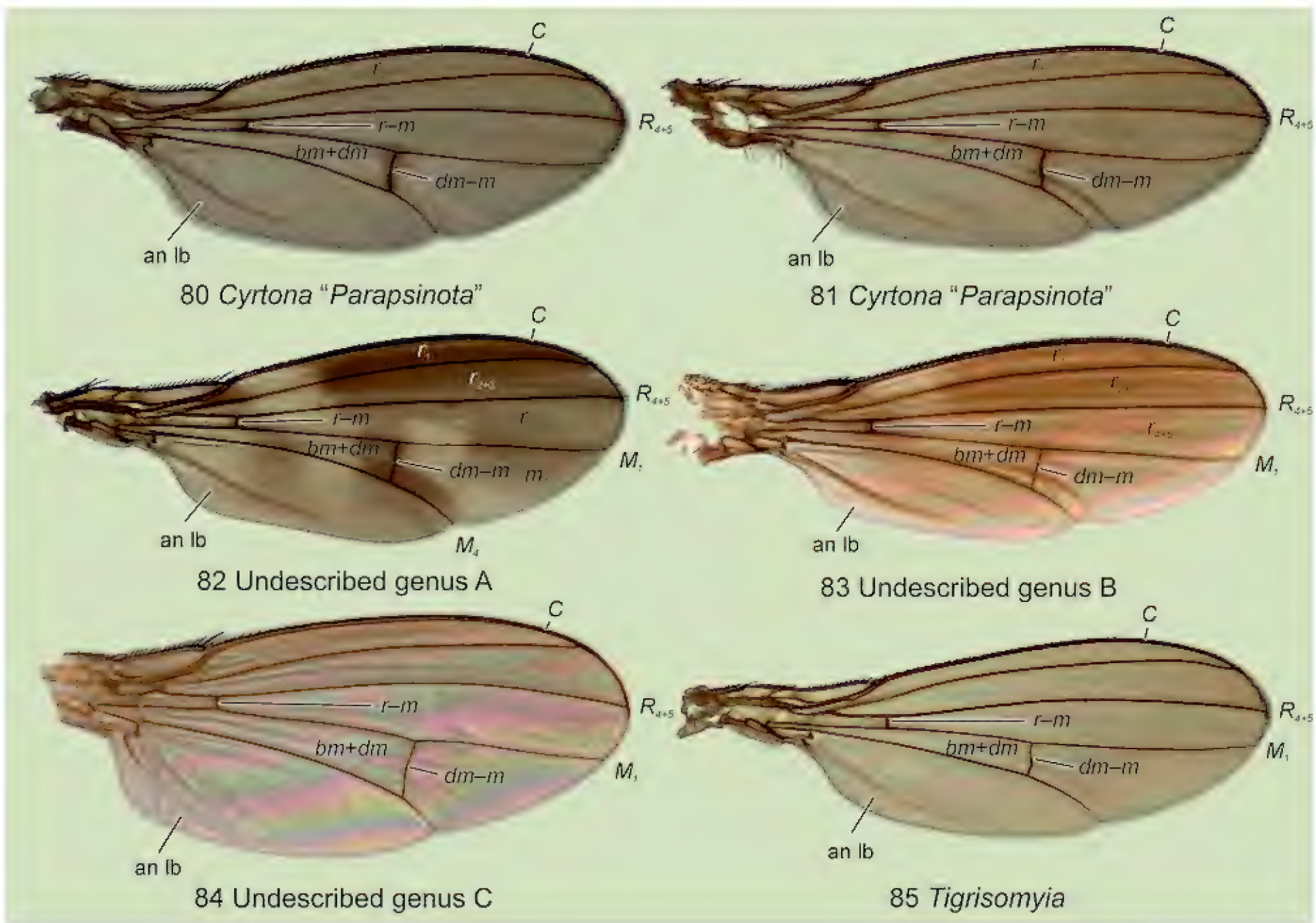
Figs 103.72–79. Wings of Curtonotidae (dorsal views): (72) *Axinota quasimodoi* Kirk-Spriggs; (73) *Axinota* sp. (non-Afrotropical); (74) *Curtonotum freidberg* Kirk-Spriggs; (75) *Cyrtona* (*s.l.*) *capensis* Hackman; (76) *Cy.* (*s.l.*) *consobrina* Hackman; (77) *Cy.* (*s.s.*) *pictipennis* (Thomson); (78) *Cy.* (*s.s.*) *appendiculata* Séguy; (79) *Cyrtona* (*s.s.*) sp. Figs 72–79 (Kirk-Spriggs & Wiegmann 2013, figs 38, 39, 174, 45, 46, 41–43, respectively © Magnolia Press).

Abbreviations: an lb – anal lobe; aux vn – auxiliary vein; *bm+dm* – basal medial cell + discal medial cell; *br* – basal radial cell; *c* – costal cell; *C* – costal vein; co sp – costal spine; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *dm–m* – discal medial crossvein; hum brk – humeral break; M_1 – first branch of media; m_1 – first medial cell; M_4 – fourth branch of media; m_4 – fourth medial cell; R_1 – anterior branch of radius; r_1 – first radial cell; r_{2+3} – second + third radial cell; R_{2+3} – second branch of radius; r_{4+5} – fourth + fifth radial cells; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Sc* – subcostal vein; sc brk – subcostal break.

Kirk-Spriggs, 2013 and *Cu. unicuspis* Kirk-Spriggs, 2013 all occurred at rest together in a single burrow, as did *Cu. bicuspis*, *Cu. cuthbertsoni* (*sensu stricto*) and *Cu. unicuspis* in another (Kirk-Spriggs & Wiegmann 2013).

Kirk-Spriggs & Freidberg (2007) noted that although roosting in mammal burrows appears to be a widespread behaviour, at least in the Afrotropical species of *Curtonotum*, there is no proven reliance on mammals or their dung and it is likely that adult flies are crepuscular or nocturnal; only roosting in such situations to avoid daytime heat, especially in the arid and hyperarid deserts in which many roosting species occur. Crepuscular or nocturnal habits in Afrotropical species are further indicated by the fact that five species were recorded as being collected at light, *i.e.*, *Cu. gonzo* Kirk-Spriggs, 2013, *Cu. maculiventris*, *Cu. simile*, *Cu. uncinatum* and *Cu. unicuspis*. Species of the *Cu. uncinatum* species-group have been observed exiting disused and collapsed pit latrines at dawn in the Zambezi Region of Namibia and *Cu. bicuspis*, *Cu. uncinatum* and *Cu. unicuspis* were attracted to decomposing fungi bait at dawn in the Kavango Region of Namibia. *Curtonotum tsacas* Kirk-Spriggs, 2013 roosts during daylight in natural and man-made hollows in closed-canopy coastal forests in South Africa (Kirk-Spriggs & Wiegmann 2013). Crepuscular activity is also evident in other genera of Curtonotidae and at least five species of *Cyrtona sensu lato* were collected just before dawn (while still dark) by sweeping on the foothills of Table Mountain, South Africa (A.H. Kirk-Spriggs, pers. obs.).

Neotropical species are found in a variety of humid environments, including riparian habitats in dry forests, freshwater and marine shorelines and forest openings in primary rainforests and high elevation cloud forests. Some species have been found on dung baits and in association with trees falls near sea level and both sexes reliably appear at branch tips before dusk on isolated floodplain trees and shrubs. Adults have also been



Figs 103.80–85. Wings of Curtonotidae (dorsal views): (80) *Cyrtona "Parapsinota" albomacula* (Curran); (81) *Cy. "Parapsinota" sublineata* Duda; (82) Undescribed genus A; (83) Undescribed genus B; (84) Undescribed genus C; (85) *Tigrisomyia amnoni* Kirk-Spriggs. Figs 80–82, 85 (Kirk-Spriggs & Wiegmann 2013, figs 47, 48, 40, respectively © Magnolia Press), Figs 83, 84 (© Trustees of Natural History Museum, London).

Abbreviations: an lb – anal lobe; *bm+dm* – basal medial cell + discal medial cell; *C* – costal vein; *dm–m* – discal medial crossvein; M_1 – first branch of media; m_1 – first medial cell; M_4 – fourth branch of media; r_1 – first radial cell; r_{2+3} – second + third radial cell; r_{4+5} – fourth + fifth radial cells; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein.

observed feeding on unidentified fragments of decomposing material on leaf surfaces (Klymko & Marshall 2011, fig. 12). Schmitz *et al.* (2007) reported collecting over 45,826 curtonotids in mangrove forests of southern Brazil, using banana-baited traps hung from trees. Fischer (1933) used traps baited with fruit juices (*i.e.*, banana, pear and peach) and vinegar to collect the type series of *Cu. punctithorax* Fischer, 1933 (Klymko & Marshall 2011).

Published information on the immature stages of the genus *Curtonotum* was reviewed by Ferrar (1987: 133), Kirk-Spriggs (2008*b*) and Meier *et al.* (1997). Klymko & Marshall (2011), reported that the puparium of an undescribed Neotropical species in the *Curtonotum murinum* species complex from Peru was dug from soil associated with *Philanthus* F. (Hymenoptera: Crabronidae) nests and suggested that they may develop as kleptoparasites on the paralysed bees with which the nest was stocked. This breeding medium is similar to that of the known associations of Afrotropical species of the genus, which develop in subterranean damaged locust and grasshopper egg pods. Greathead (1958) was the first to describe the immature stages of what was then believed to represent *Cu. cuthbertsoni* (as *Cyrtonotum*), from material reared from Eritrea. He described the third-instar larva using light microscopy and provided line drawings illustrating the cephaloskeleton (as buccopharyngeal armature), the prothoracic and posterior spiracles, the anterior and posterior ends (lateral) and the posterior end from behind. He also provided supplementary, unillustrated descriptions of the second-instar larva and puparium.

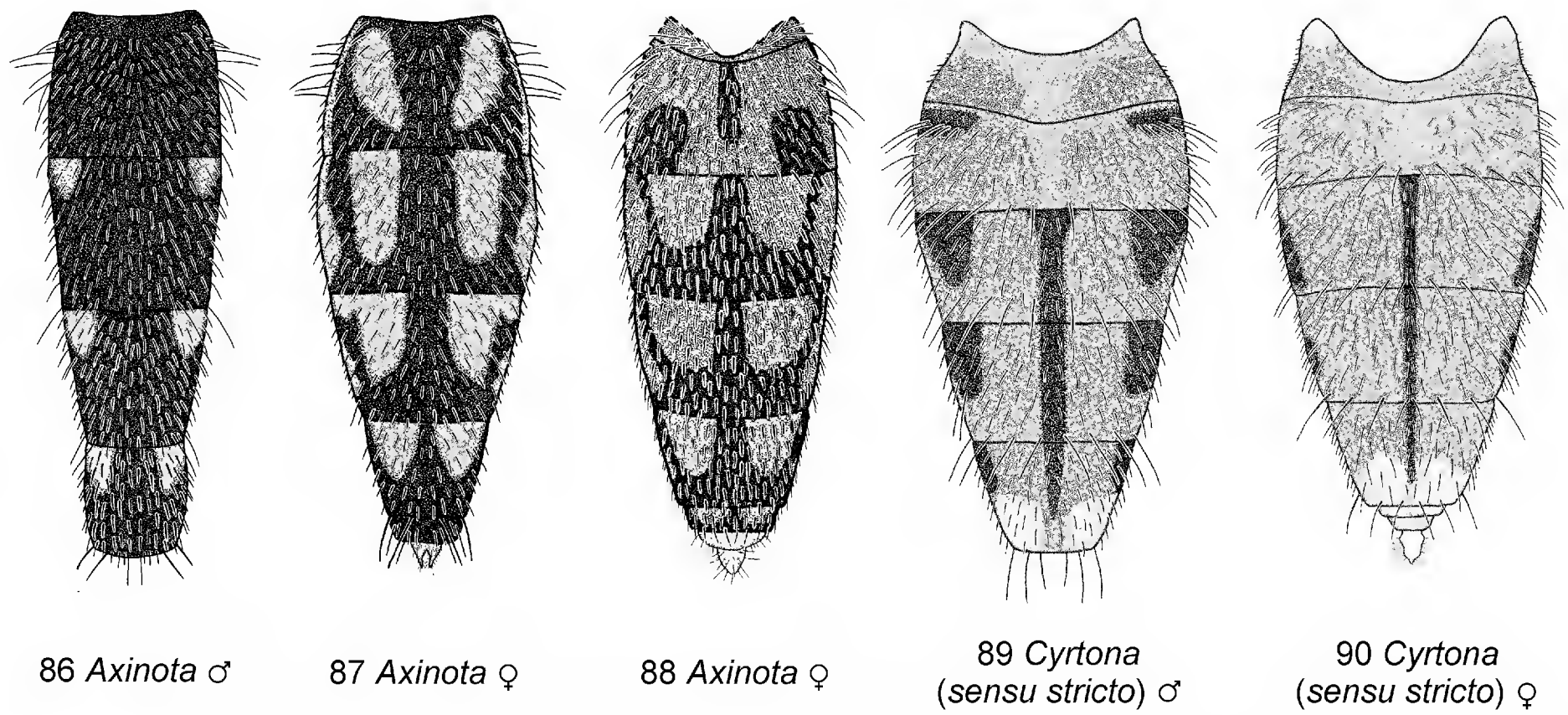
Most recently, Kirk-Spriggs (2008*b*) reviewed knowledge of the immature stages of the genus *Curtonotum* and described the damaged larva of *Cu. saheliense* (?), re-described the puparium of *Cu. simile* and described the puparium of *Cu. saheliense*.

Economic significance

Greathead (1958) recorded *Curtonotum saheliense* (as *Cyrtonotum cuthbertsoni*) from material reared from damaged egg pods of the desert locust, *Schistocerca gregaria* (Forskål) (Orthoptera: Acrididae), in Eritrea. He concluded that they were probably saprophagous on damaged, putrefying egg pods, rather than being truly parasitic and further noted that the damage they caused to locust eggs was minimal, as compared to insects (including other Diptera) causing primary attack. Braack (1986) recorded *Curtonotum bicuspis* (as *Curtonotum cuthbertsoni*) visiting mammal carcases in South Africa, although the species was later listed as "Adventive (= visiting unpredictably)" by Villet (2017: 179), indicating that the species probably has little or no forensic significance. No other cases of economic importance are recorded in the literature.

Classification

Curtonotids have been assigned to various families in the past, including the Heleomyzidae (Perris 1839), Opomyzidae (as Geomyzidae) (Czerny 1903; Osten Sacken 1882), Drosophilidae (e.g., Dwivedi & Gupta 1979; Hendel 1932, 1933; Malloch 1930), Diastatidae (Duda 1924; Meigen 1830: 94; Okada 1960, 1966) and Ephydridae. Enderlein (1914: 272, 1917) placed them as a subfamily (Cyrtonotinae) of the Ephydridae. Hendel (1917, 1928), regarded them as a subfamily (Cyrtonotinae) of the Drosophilidae, followed by Sturtevant (1921: 52), Malloch (1930), Hendel (1932), Curran (1933, 1934: 327), Greathead (1958) and several other authors. Duda (1934) gave them full familial rank, which has been followed by the majority of subsequent workers, including: Delfinado (1969), Griffiths (1972: 108), Hackman (1960: 381), Hennig (1958, 1971, 1973), Kirk-Spriggs (2007, 2008*a*, *b*, *c*,

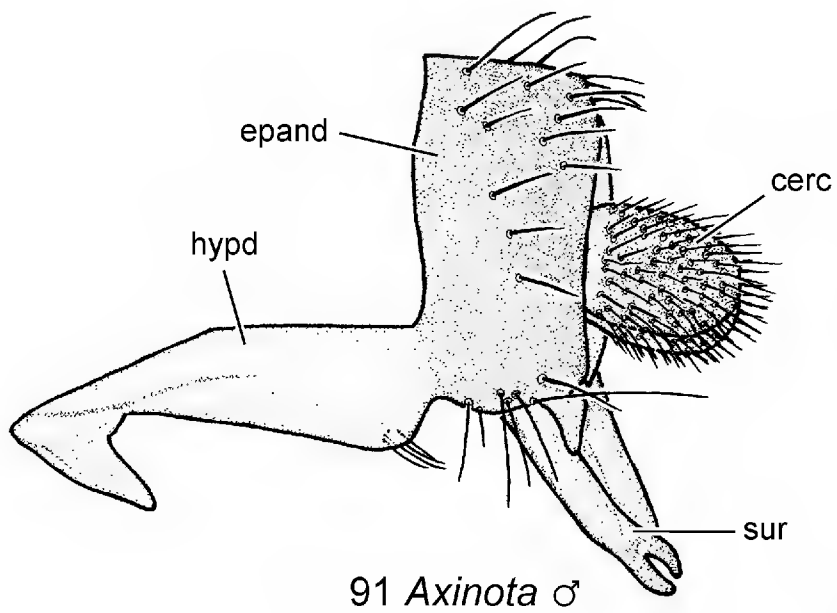


Figs 103.86–90. Abdomens of Curtonotidae (dorsal views): (86) *Axinota quasimodoi* Kirk-Spriggs, dorsal view ♂; (87) *A. fuscipennis* (Macquart) ♀; (88) *A. kyphosis* Kirk-Spriggs ♀; (89) *Cyrtona* (*s.s*) *appendiculata* Séguy ♂; (90) *Cy.* (*s.s.*) *pictipennis* (Thomson) ♀. Figs 86–88 (Kirk-Spriggs 2010*a*, figs 14, 13, 16, respectively).

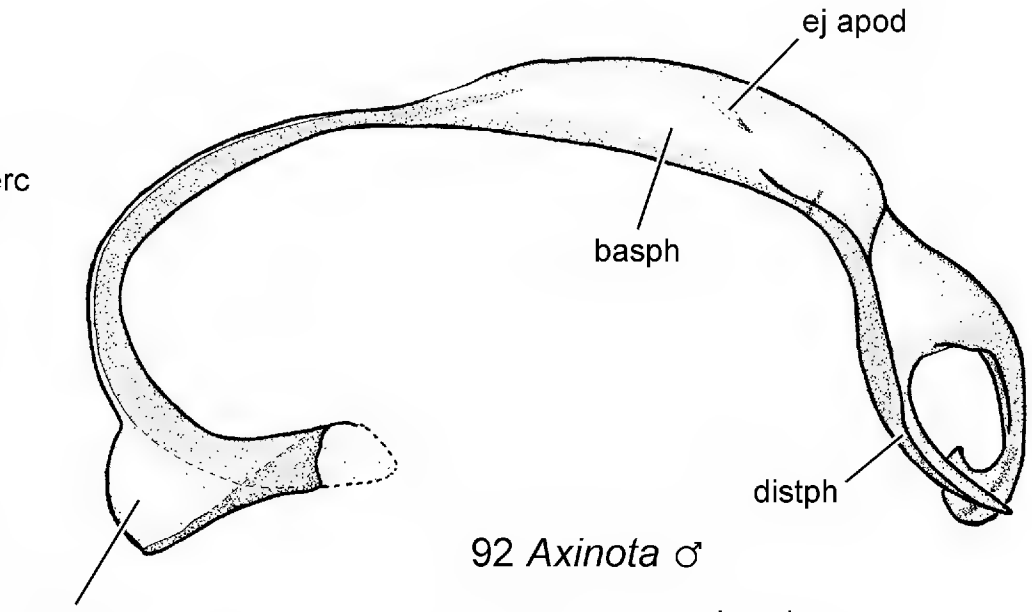
2010*a*, *b*, 2011), Kirk-Spriggs & Freidberg (2007), Kirk-Spriggs & Wiegmann (2013), Klymko & Marshall (2011), Marshall *et al*. (2010), McAlpine (1987: 1007, 1989: 1487), Meier *et al*. (1997), Papp (1984: 221, 1998: 397), Pollock (1996, 2002), Tsacas (1974, 1977), Wirth (1965: 759, 1975: 1, 1977: 340) and Wirth & Tsacas (1980: 671).

Hennig (1958: 662) regarded the Ephydroidea (as Drosophiloidea) to include the families Camillidae, Curtonotidae, Diastatidae, Drosophilidae and Ephydridae, considering the superfamily to be "… the best substantiated monophyletic part-groups of the Schizophora" (translation G.H. Harder). In a groundplan approach, Hennig noted the following synapomorphic characteristics of the Curtonotidae in relation to the basic groundplan of the Schizophora: 1.) The costa is disrupted at two points; 2.) Proclinate orbital seta are in evidence; 3.) The anal cell is short, cu1b is recurved; 4). The anal vein is shortened, does not reach the wing margin (figs 346–347)" (translation G.H. Harder). Although he noted that the adduced synapomorphic characteristics did not provide a definitive association to any family in the Drosophiloidea, he nevertheless considered the Curtonotidae to be a sister-group of the Drosophilidae.

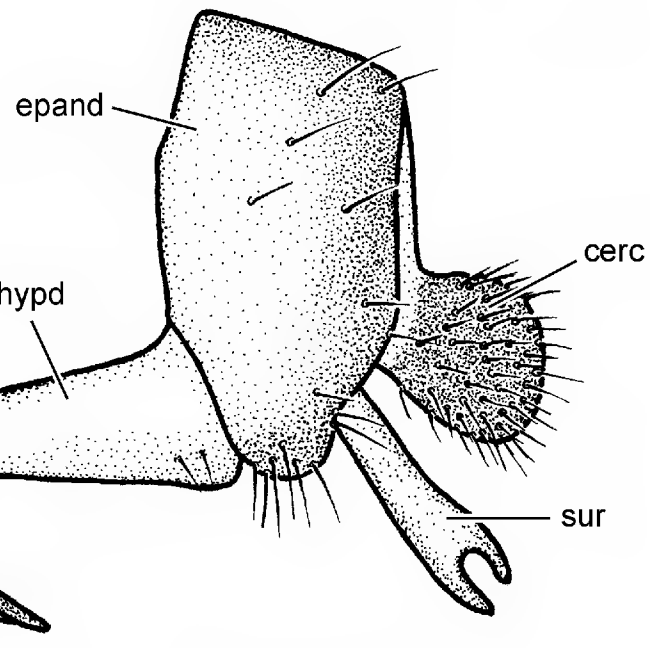
Hennig (1971) further discussed the phylogenetic significance of antennal development at some length. He noted that in *Camilla* Haliday (Camillidae), *Curtonotum* and *Drosophila* Fallén (Drosophilidae) the lobe of the postpedicel is completely enclosed in the interior of the pedicel, presumably due to the fact that the outer wall became enlarged, and its distal margin assumed a closed elliptic form. The margins of the dorsolateral notch on the pedicel presumably moved proximally, but are not fused, so that a long slit was formed. He noted that such peculiarities in antennal development can be regarded as an additional character supporting the assumption that the Ephydroidea (as Drosophiloidea) are a monophyletic group. He further noted that antennal structure also indicates that the Camillidae are more closely related to the Curtonotidae and Drosophilidae than to the Ephydridae and that this assumption is supported, perhaps, by the fact that the proclinate frontoorbital seta in the Curtonotidae, Drosophilidae and Camillidae



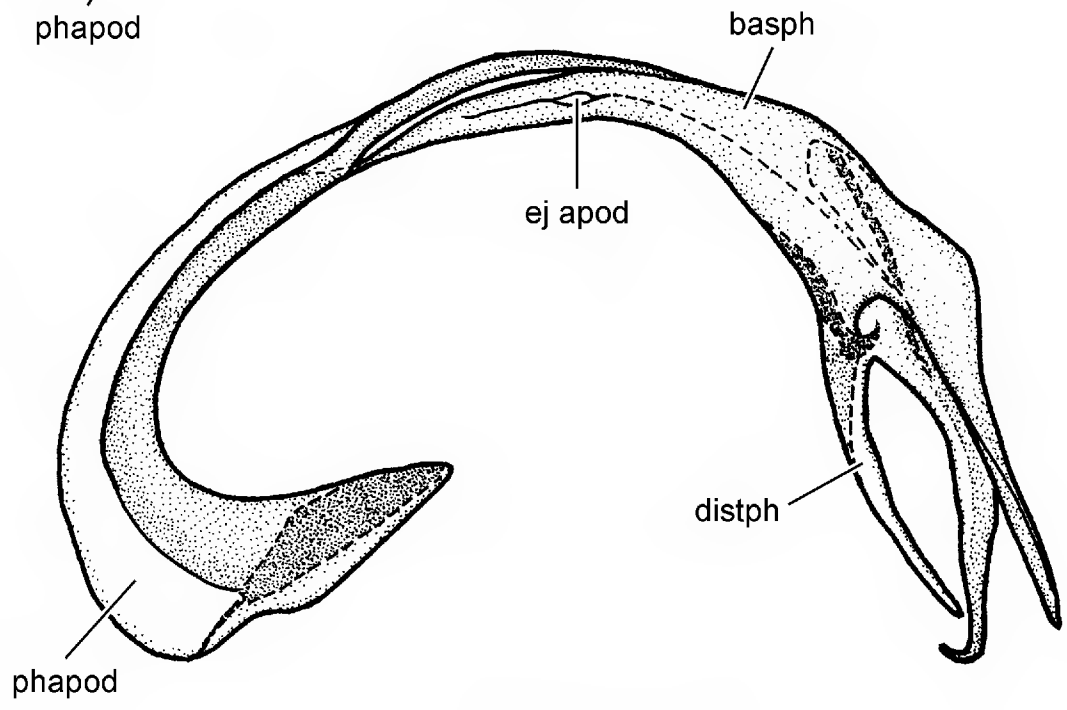
91 *Axinota* ♂



92 *Axinota* ♂



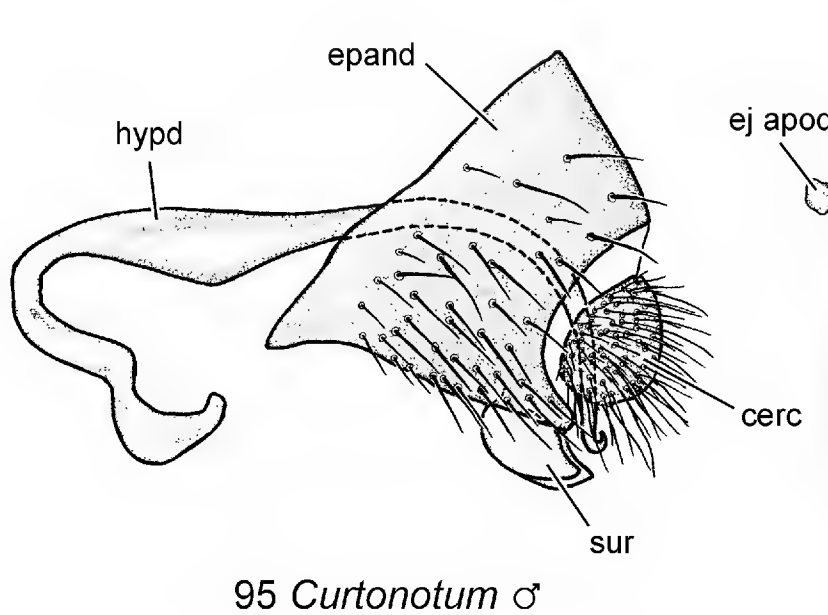
93 *Axinota* ♂



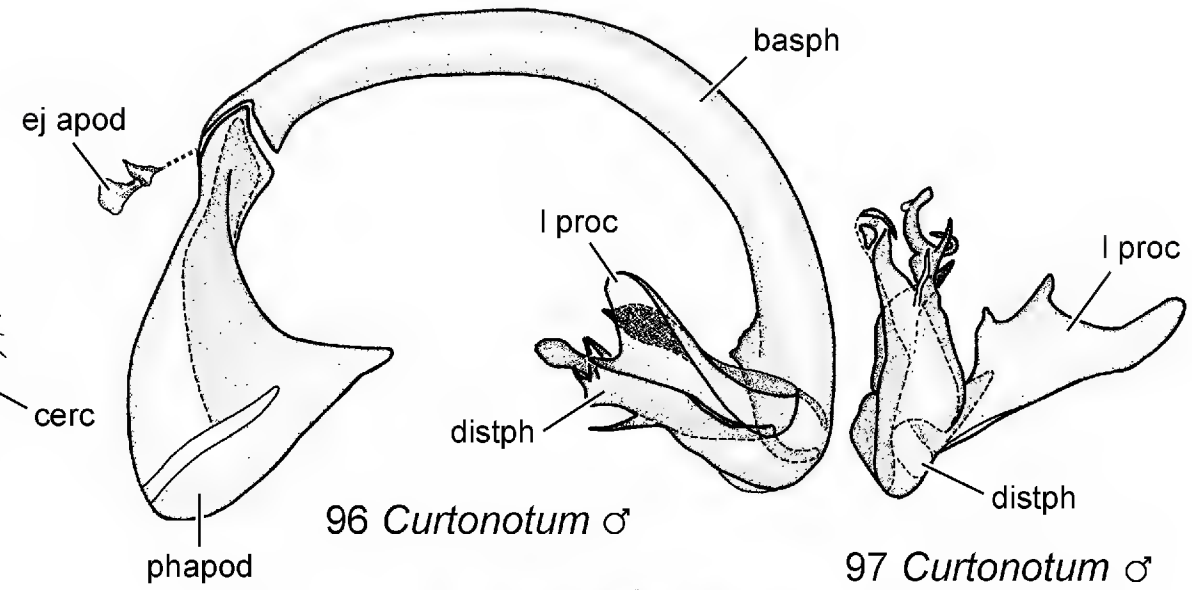
94 *Axinota* ♂

Figs 103.91–94. Male terminalia of Curtonotidae (lateral views): (91) epandrium and hypandrium of *Axinota quasimodoi* Kirk-Spriggs; (92) same, phallus, right lateral view; (93) epandrium and hypandrium of *A. kyphosis* Kirk-Spriggs; (94) same, phallus, right lateral view. Figs 91–94 (Kirk-Spriggs 2010*a*, figs 18, 22, 20, 24, respectively).

Abbreviations: basph – basiphallus; cerc – cercus; distph – distiphallus; ej apod – ejaculatory apodeme; epand – epandrium; hypd – hypandrium; phapod – phallapodeme; sur – surstylus.

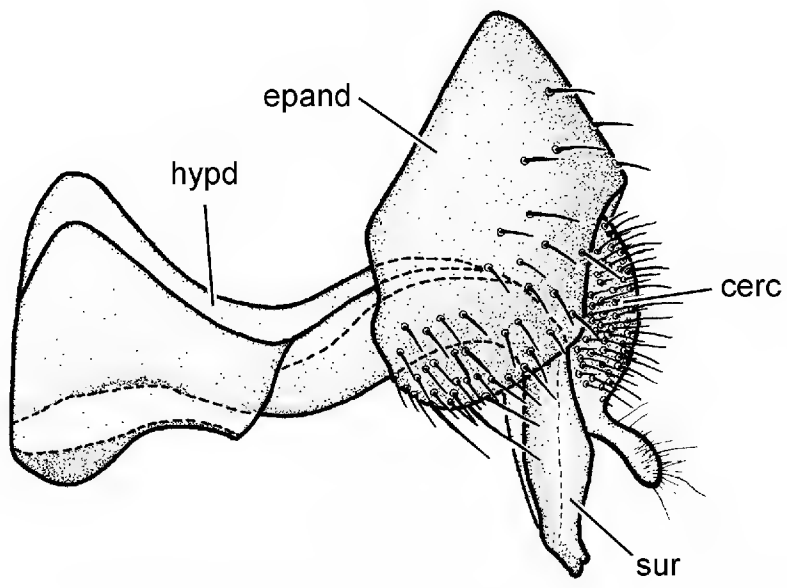


95 *Curtonotum* ♂

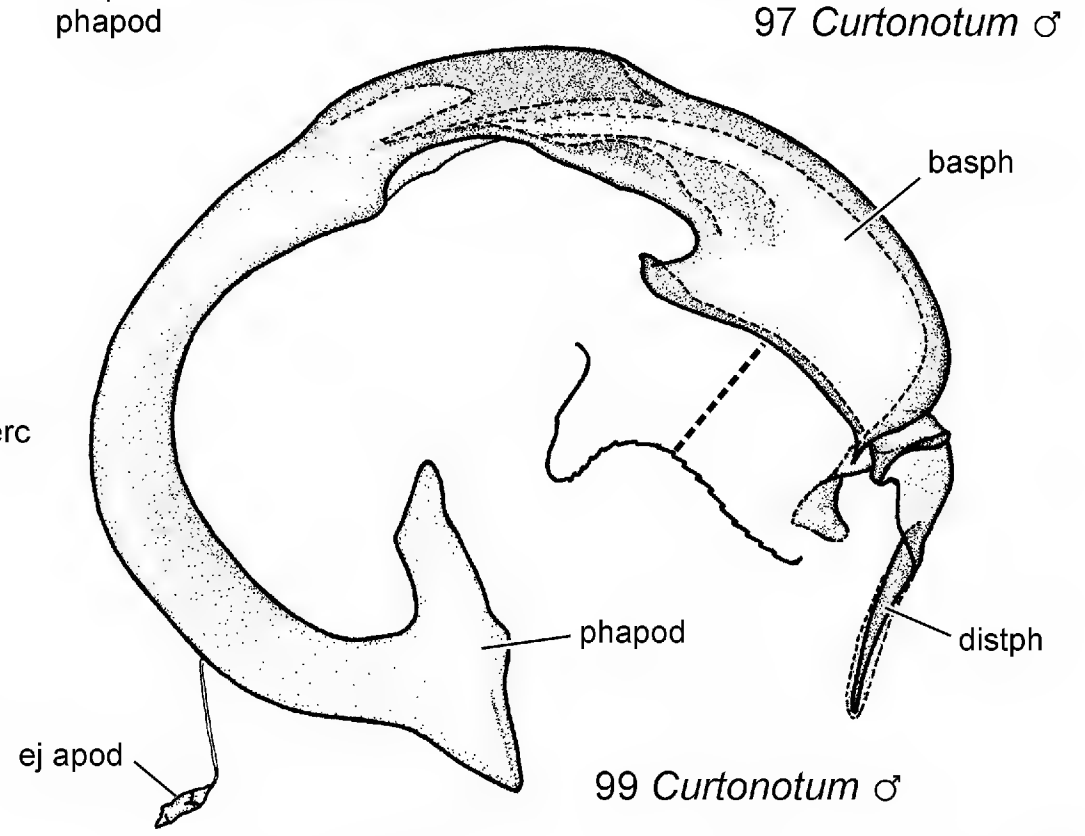


96 *Curtonotum* ♂

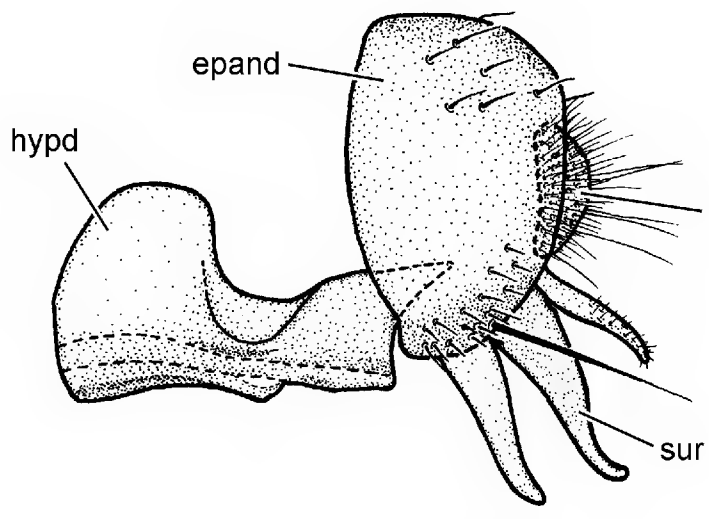
97 *Curtonotum* ♂



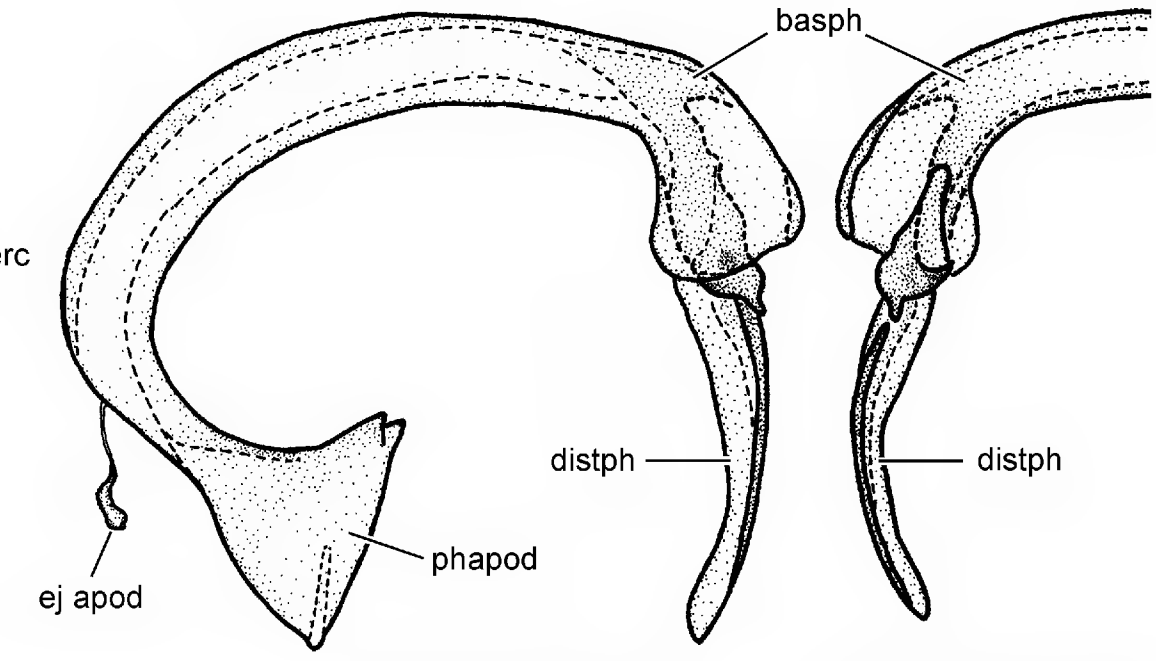
98 *Curtonotum* ♂



99 *Curtonotum* ♂



100 *Curtonotum* ♂



101 *Curtonotum* ♂ 102 *Curtonotum* ♂

Figs 103.95–102. Male terminalia of Curtonotidae: (95) epandrium and hypandrium of *Curtonotum herrero* Tsacas, lateral view; (96) same, phallus, right lateral view; (97) same, distiphallus, apical view; (98) epandrium and hypandrium of *Cu. marriott* Kirk-Spriggs, lateral view; (99) same, phallus, lateral view (inset: detail of serrated edge of basiphallus); (100) epandrium and hypandrium of *Cu. sao* Tsacas, lateral view; (101) same, basiphallus and distiphallus, right lateral view; (102) same, left lateral view. Figs 95–102 (Kirk-Spriggs & Wiegmann 2013, figs 194, 197, 200, 222, 225, 226, 249, 253, 257 © Magnolia Press).

Abbreviations: basph – basiphallus; cerc – cercus; distph – distiphallus; ej apod – ejaculatory apodeme; epand – epandrium; hypd – hypandrium; l proc – lateral process; phapod – phallapodeme; sur – surstylus.

are inserted immediately ventral to the two reclinate ones, rather than being inserted between these and the eye margin, as in the Diastatidae and Ephydridae. He thus divided the Ephydroidea into two suprafamilies, the Drosophilidea, consisting of the Camillidae, Curtonotidae and Drosophilidae, and the Ephydridea, consisting of the Diastatidae and Ephydridae.

Hennig (1973) defined the family Curtonotidae by the following: "apical plates [= orbital plates] with fronto-orbital bristles distinct from the anterior margin of the eye. Thorax strongly arched. Mesopleural bristles [= anepisternal setae] present. Postabdomen distinctly delimited from preabdomen, prehypopygial segments of the postabdomen reduced (smaller)" (translation G.H. Harder).

Griffiths (1972: 100) followed Hennig (1958, 1971, 1973) in the delimitation of the superfamily Ephydroidea (as Drosophiloidea), his concept including the families Camillidae, Campichoetidae, Curtonotidae, Drosophilidae and Ephydridae. He also regarded the Ephydroidea (*sensu* Hennig 1958) to be (p. 100) "… one of the most surely grounded monophyletic groups in the Schizophora." He noted the following synapomorphic conditions in respect to the groundplan of the Schizophora: 1.) 3rd antennal article [= postpedicel] bearing long dorsolateral process which projects within the 2nd article [pedicel]; 2.) Aedeagus [phallus] (♂) grossly enlarged, curved downwards anteriorly where it is fused with the aedeagal apodeme [= phallapodeme] (fig. 40); 3.) 6th and 7th terga (♂) reduced, much shorter than preceding terga; 4.) 8th sternum (♂) completely lost; 5.) Second costal break present (shortly beyond humeral crossvein) [following Hennig 1958]; 6.) Base of m_4 (= "tb", basal crossvein [= *bm–m* crossvein]) lost [following Hennig 1958]; 7.) Spermathecae (♀) long and slender [following Hennig 1958]. Griffiths made no attempt to divide the Drosophiloidea into "prefamilies", as Hennig (1958) did not discuss the Campichoetidae when proposing his subdivisions of the superfamily.

McAlpine (1989: 1486) followed the previous interpretations of Hennig (1958, 1971, 1973) and Griffiths (1972) in including the five families Camillidae, Curtonotidae, Diastatidae, Drosophilidae and Ephydridae in his concept of the Ephydroidea and corrected the usage of the superfamilial name Ephydroidea over Drosophiloidea. McAlpine disagreed with Hennig's concept of suprafamilies, however, being of the view that the primary evolutionary dichotomy in the Ephydroidea lay between the Curtonotidae and the remaining four families. This view was based on the fact that the subcostal vein (*Sc*) is complete and free from vein R_1 in the Curtonotidae (plesiomorphic condition), as opposed to being apically reduced and fused with vein R_1 in the remaining four families (synapomorphic condition). He noted that the Curtonotidae possess a peculiar set of plesiomorphic and synapomorphic character states, which sets the Curtonotidae apart from the remainder of the Ephydroidea. He stated that almost all groundplan characters of the Ephydroidea are expressed in the groundplan of the Curtonotidae and listed seven characters for the family that he regarded as unequivocally synapomorphic: 1). Postpronotum with supplementary bristles; 2). Scutum usually strongly humped; 3). Cells *bm* and *dm* confluent, *i*.e., crossvein *bm–m* absent; 4). A_1 [= *CuA+CuP*] secondarily lengthened; 5). Sternite 8 of the male absent; 6). Aedeagus [= phallus] enlarged, C-shaped, distiphallus anteroventrally directed and; 7). Aedeagal apodeme [= phallapodeme] closely and broadly joined to basiphallus. He concluded that these seven synapomorphic characters, together with six other listed synapomorphic conditions attest to the monophyly of the family and suggested that the Curtonotidae is probably sister-group of the remainder of the Ephydroidea.

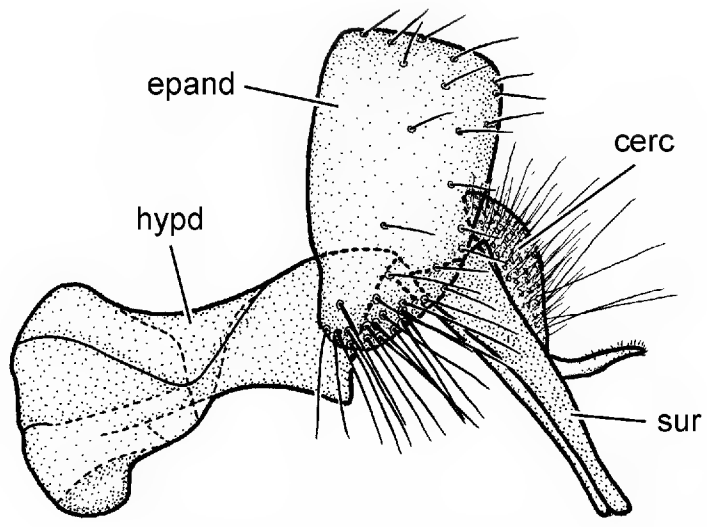
All of the above published studies took a groundplan approach and presented matrices of characters. Grimaldi (1990) was the first to attempt a morphological cladistic analysis of the Ephydroidea. He reassessed the characters noted by Hennig (1958, 1971, 1973), Griffiths (1972), and McAlpine (1989: 1488); included selected characters noted in a matrix format by Chandler (1987), for the Diastatidae and Campichoetidae and included additional characters of his own. This study resulted in three equally parsimonious hypotheses of families in the Ephydroidea. Both trees 1 and 2 (p. 23, figs 8, 9) infer that the Curtonotidae are sister to the remainder of the Ephydroidea, while Grimaldi's preferred tree 3 (p. 23, fig. 10), infers that the Drosophilidae + Curtonotidae are the sister-group to the remainder of the Ephydroidea.

Pollock (2002) assembled an alternative groundplan character matrix for what he termed "Ephydroidea *sensu lato*", being in his view the six families then ascribed to "Ephydroidea *sensu stricto*", plus the calyptrate families Gasterophilidae, Hippoboscidae, Glossinidae and Oestridae. Pollock considered the Oestridae and Hippoboscidae to be "derived from early ephydroids" (p. 1740). Evidence supporting such a theory was unconvincing, however, and published molecular phylogenetic studies of the Calyptratae specifically (e.g., Kutty *et al*. 2010), the Hippoboscoidea, four additional families of calyptrates and the Drosophilidae (Petersen *et al*. 2007) and the Diptera in general (Wiegmann *et al*. 2011), lend no support to such a theory and this must, therefore, be regarded as ungrounded.

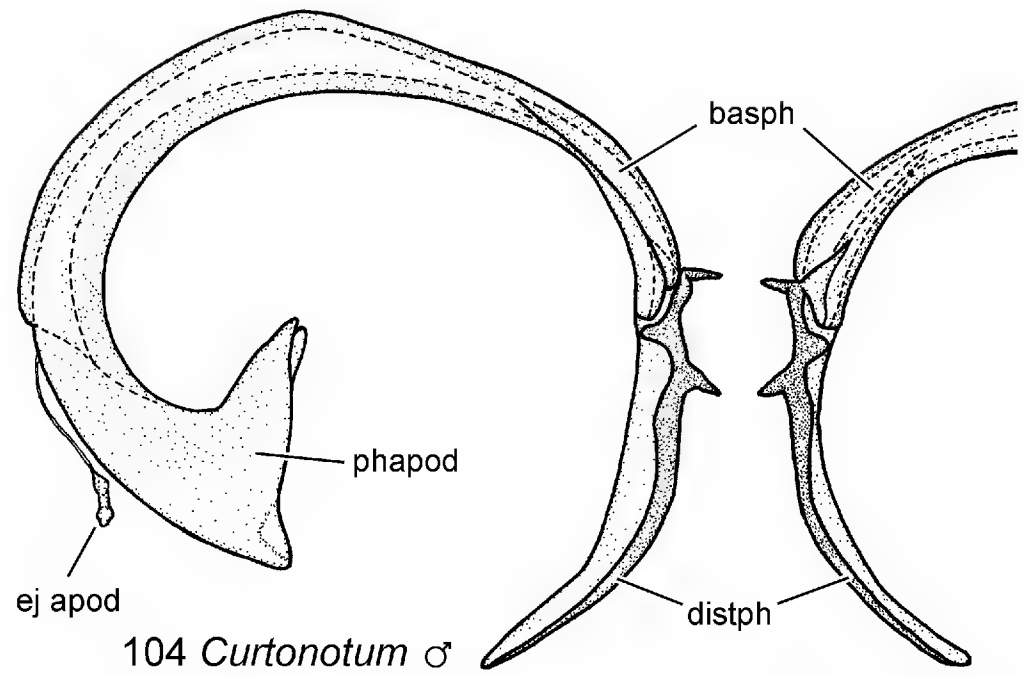
In a more recent study, Wiegmann *et al*. (2011) provided a phylogenetic estimate of fly relationships based on molecular data from 149 of the 157 families globally. Results of this study differs from previous interpretations of relationships within the superfamily and suggest that (Drosophilidae + Braulidae + Cryptochetidae) are sister to the remainder of the Ephydroidea (Camillidae + (Curtonotidae + Diastatidae)), except for the Ephydridae.

Recent molecular resolution of the phylogeny of the Ephydroidea that includes the enigmatic family Mormotomyiidae (Wiegmann *et al*. in prep.), has (Camillidae + Curtonotidae + Diastatidae) as sister to the remainder of the Ephydroidea (Braulidae + Drosophilidae + Cryptochetidae), except for the Ephydridae and Mormotomyiidae. In the most recently published molecular study of schizophoran flies, Bayless *et al*. (2021) recovered Curtonotidae as sister-group to Diastatidae.

Meier *et al*. (1997) proposed some hypotheses regarding phylogenetic relationships of the three genera of Curtonotidae described to that date. These hypotheses were based on the form and surface texture of the spermathecae. They noted that three types of spermathecae occur in the genus *Curtonotum*: 1). Slender, elongate, sclerotised spermathecae that are studded with small protuberances. To this group they ascribed the Nearctic species *Cu. helvum*, the Neotropical type species of the genus, *Cu. taeniatum* Hendel, 1913 and the three Afrotropical species in the *Curtonotum striatifrons* species-group (*sensu* Tsacas 1977). 2). Obclavate spermathecae (*i*.e., having

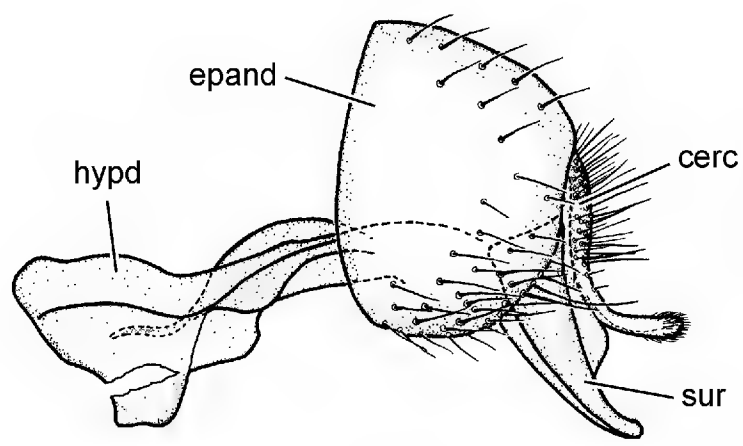


103 *Curtonotum* ♂

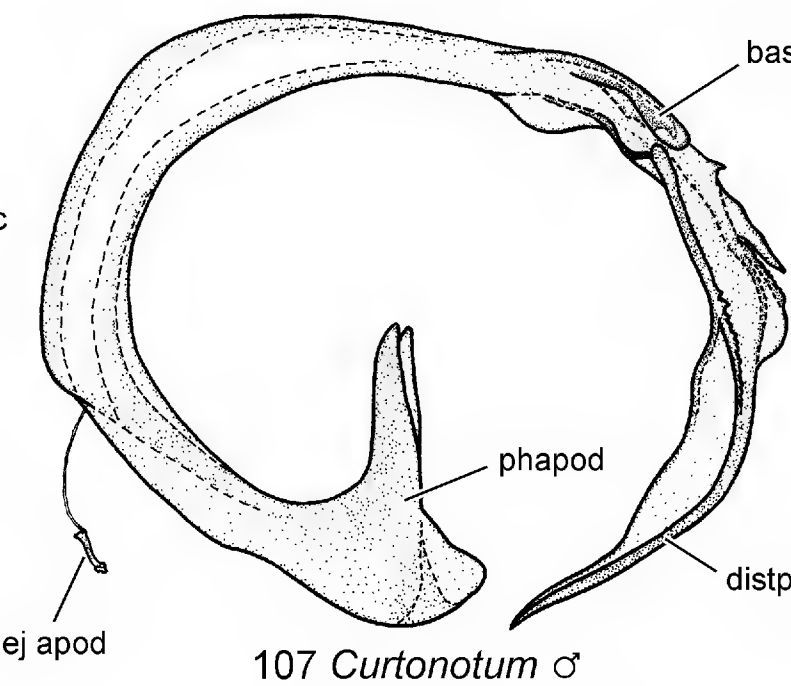


104 *Curtonotum* ♂

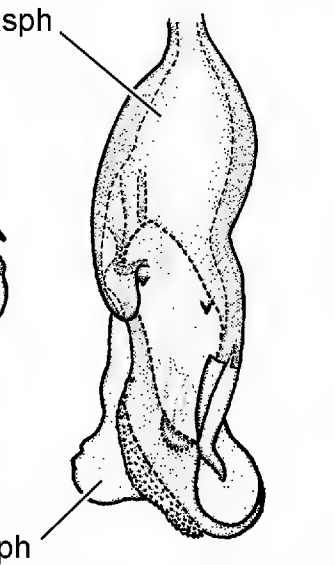
105 *Curtonotum* ♂



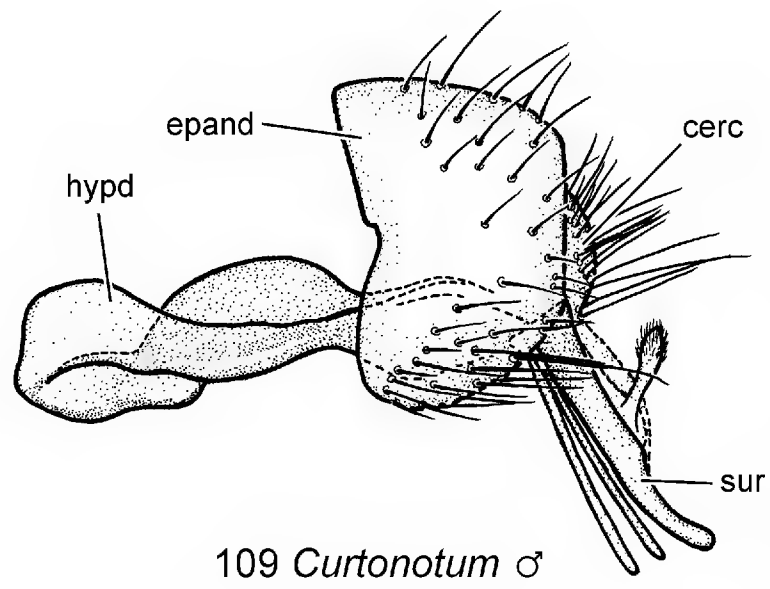
106 *Curtonotum* ♂



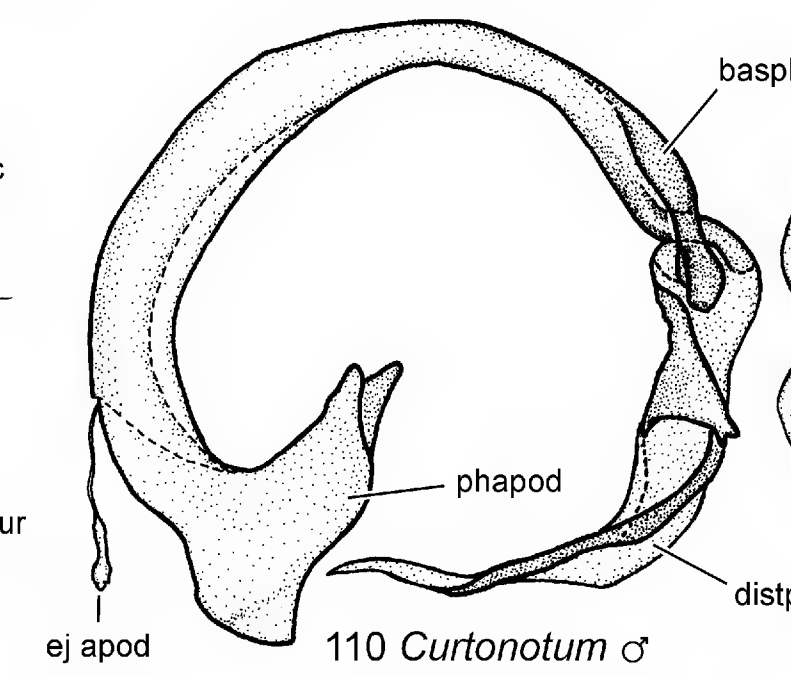
107 *Curtonotum* ♂



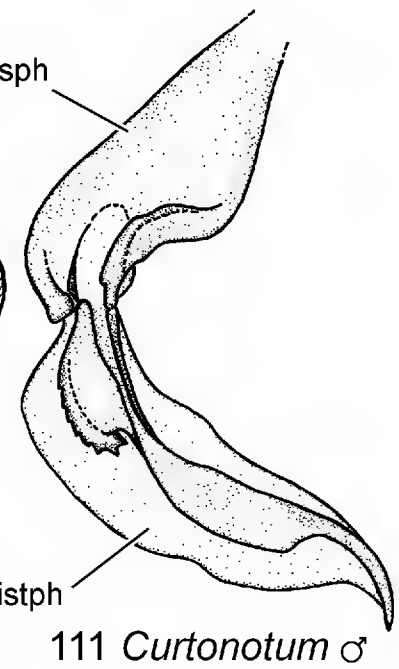
108 *Curtonotum* ♂



109 *Curtonotum* ♂



110 *Curtonotum* ♂

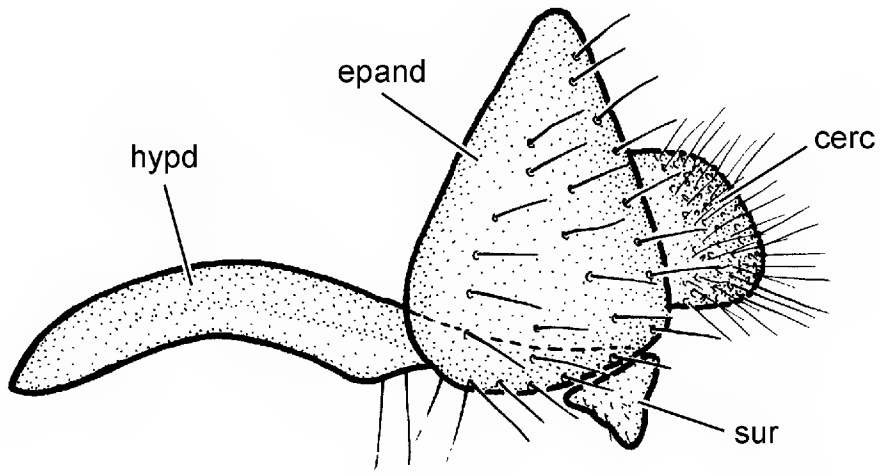


111 *Curtonotum* ♂

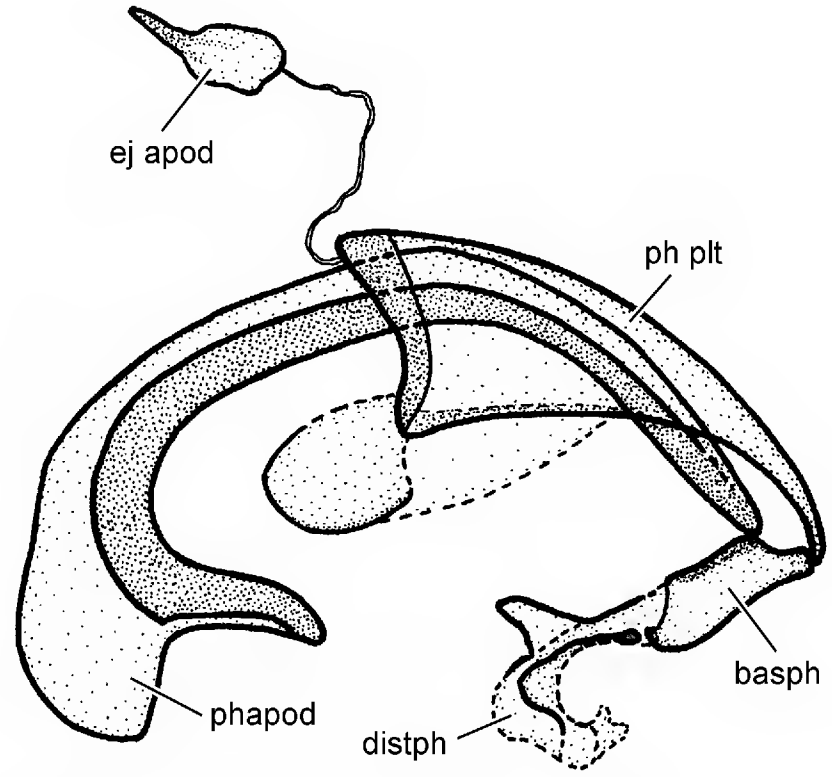
Figs 103.103–111. Male terminalia of Curtonotidae: (103) epandrium and hypandrium of *Curtonotum bicuspis* Kirk-Spriggs, lateral view; (104) same, phallus, right lateral view; (105) same, phallus, left lateral view; (106) epandrium and hypandrium of *Cu. stuckenbergi* Tsacas, lateral view; (107) same, phallus, right lateral view; (108) same, basiphallus and distiphallus junction, dorsal view; (109) epandrium and hypandrium of *Cu. coronaeformis* Kirk-Spriggs, lateral view; (110) same, phallus, right lateral view; (111) same, basiphallus and distiphallus junction, dorsal view. Figs 103–105 (Kirk-Spriggs & Wiegmann 2013, figs 268, 271, 274 © Magnolia Press), Figs 106–111 (Kirk-Spriggs 2011, figs 56, 59, 62, 66, 69, 72).

Abbreviations: basph – basiphallus; cerc – cercus; distph – distiphallus; ej apod – ejaculatory apodeme; epand – epandrium; hypd – hypandrium; phapod – phallapodeme; sur – surstylus.

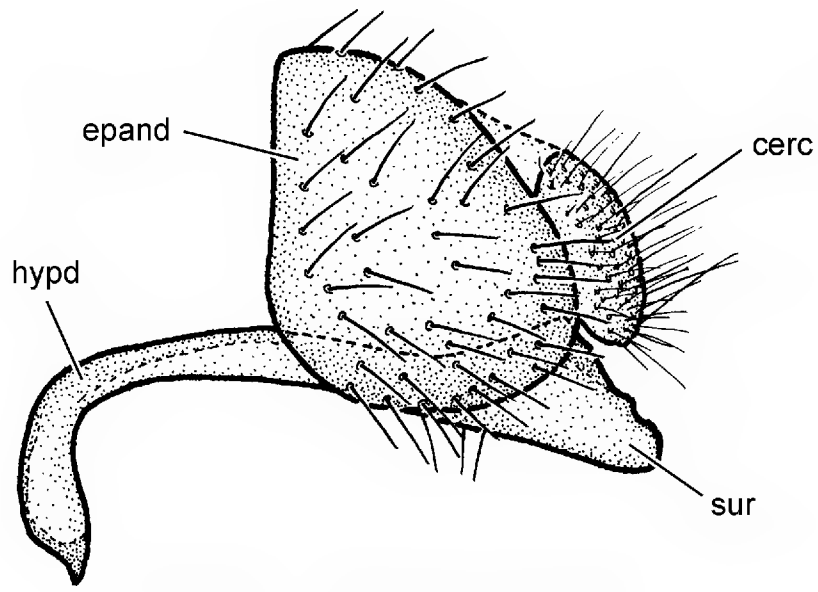
a wide base tapering to a point) with a wrinkled (rugose) surface (see Kirk-Spriggs 2008c: 246). To this group they ascribed the *Curtonotum cuthbertsoni* species-group (*sensu* Tsacas 1977) and the "… ten Madagascan species" (p. 12) (only seven of which were then named species (Kirk-Spriggs 2011)). They further discussed the illustrations of the spermathecae of the Oriental species *Cu. ceylonense* Delfinado, 1969 by Delfinado (1969, fig. 25) and concluded that these have the same general shape, but were illustrated from a different orientation. The spermathecal duct is not illustrated, but it is apparent that these are of the same type. Indeed, Tsacas (1977) ascribed the three species of *Curtonotum* occurring in the Oriental Region to the *cuthbertsoni* species-group. 3). Small, subspherical spermathecae that are studded with small protuberances. They noted that this condition is only known in the Oriental species *Curtonotum angustipennis* (de Meijere, 1911). On the basis of this information, Meier *et al.* (1997) stated that *Axinota* is the sister-group to *Curtonotum* + *Cyrtona*, due to the assumed plesiomorphic condition of the spermatheca of (the as then undescribed), *Axinota kyphosis* Kirk-Spriggs, 2010 from Madagascar. The spermathecae of this species are small and doliform (*i.e.*, short cylindrical to round), with a deep basal and shallow, apical invagination. This is the most common spermathecal state in the Drosophilidae; the putative sister family of Curtonotidae, as proposed by Grimaldi (1990) and thus thought to represent the groundplan condition for Curtonotidae. They noted, however, that in the Oriental species of *Axinota* the spermathecae are rounded or mushroom-shaped and sclerotised with a smooth



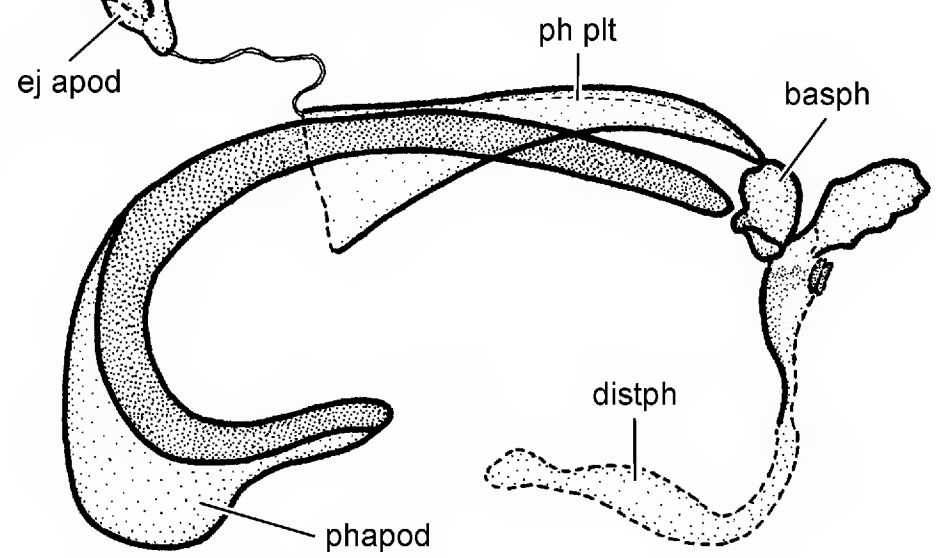
112 *Cyrtona* (*sensu lato*) ♂



113 *Cyrtona* (*sensu lato*) ♂



114 *Cyrtona* (*sensu lato*) ♂



115 *Cyrtona* (*sensu lato*) ♂

Figs 103.112–115. Male terminalia of Curtonotidae (lateral views): (112) epandrium and hypandrium of *Cyrtona* (*s.l.*) *capensis* Hackman; (113) same, phallus, right lateral view; (114) epandrium and hypandrium of *Cy.* (*s.l.*) *consobrina* Hackman; (115) same, phallus, right lateral view. Figs 112–115 (Kirk-Spriggs & Wiegmann 2013, figs 63, 66, 67, 70 © Magnolia Press).

Abbreviations: basph – basiphallus; cerc – cercus; distph – distiphallus; ej apod – ejaculatory apodeme; epand – epandrium; hypd – hypandrium; ph plt – phallic plate; phapod – phallapodeme; sur – surstylus.

surface and further suggested that the presence of spinules on the spermatheca of *Cyrtona* and *Curtonotum* (absent in examined *Axinota* and the groundplan of Drosophilidae) represents another synapomorphy for these two genera.

Pollock (2002) tentatively proposed *Cyrtona* as the sister-group to a clade made up of *Curtonotum* + *Axinota* as the last two named genera both exhibit phallic asymmetry and a reduction of the pregenital sclerites.

In a first morphological phylogenetic analysis of Curtonotidae, the New World species of *Curtonotum* were treated by Klymko & Marshall (2011), who recognised *Curtonotum* + *Axinota* as forming a monophyletic group. They noted that unlike *Cyrtona*, with its expanded tergite 7, *Axinota*, with its sexually dimorphic frons, and *Tigrisomyia* with its strikingly marked thorax and highly derived male terminalia, *Curtonotum* has no obvious synapomorphies, with the possible exception of the spinose costal vein. They noted that this condition is absent in *Cyrtona* and is only expressed in the two Afrotropical species of the *Axinota fuscipennis* species-group (*sensu* Kirk-Spriggs 2010a) and is generally absent in the other families within Ephydroidea, the Diastatidae (including Campichoetidae) being an exception. This condition was considered plesiomorphic for the Ephydroidea by McAlpine (1989: 1486), given its scattered occurrence and its general absence in Drosophilidae. They considered this condition to more likely be independently derived several times in the Acalyptratae and once or twice in Curtonotidae (either once in a *Curtonotum* + *Axinota* ancestor, followed by the secondary loss in most *Axinota*; or twice, once each in *Curtonotum* and *Axinota*). They concluded that *Curtonotum* in its current broad sense is probably paraphyletic with respect to *Axinota* and suggested restricting the name *Curtonotum* to a monophyletic Neotropical group. They suggested that the two Nearctic species of *Curtonotum* belong to the *anus* species-group (as first proposed by Kirk-Spriggs & Freidberg 2007), together with the Palaearctic species of the genus and provided additional characters to define the group.

Kirk-Spriggs & Wiegmann (2013) published the first comprehensive phylogeny of the entire family Curtonotidae, generated from molecular markers and morphology. The molecular data set comprised 33 taxa (30 in-group Curtonotidae; three out-groups) and four gene regions from three genes: two non-contiguous fragments from the CPSase (carbamoylphosphate synthetase) domain of the nuclear protein coding gene CAD (= CAD1 and CAD3); a fragment from the coding region of TPI (triosephosphate isomerase); and a fragment of the mitochondrial gene COI (cytochrome oxidase I). A data matrix of 62 discrete, morphological features of imagines was compiled from 75 taxa (70 in-group Curtonotidae taxa and five out-group exemplars). Results of the molecular and morphological analyses attested to the monophyly of the Curtonotidae and clearly indicated two primary clades, with *Axinota* + *Curtonotum* being sister to the remainder of the Curtonotidae. *Curtonotum sensu stricto* (*sensu* Klymko & Marshall 2011) was adopted and ten newly defined species-groups of the genus *Curtonotum sensu lato* were recognised. In this work it was substantiated that *Curtonotum* is paraphyletic with respect to *Axinota* and *Curtonotum* species outside the Neotropical Region should be regarded as *Curtonotum sensu lato*. Undescribed genus B and C, as treated in this chapter, were not included in the analyses.

Two amber fossil species of Curtonotidae are known from Miocene amber of the Dominican Republic (17–20 Mya) (Grimaldi & Kirk-Spriggs 2012), namely *Curtonotum* †*electrodominicum* Grimaldi & Kirk-Spriggs, 2012 and *Depressonotum priscum* Grimaldi & Kirk-Spriggs, 2012. A third compression fossil attributed to Curtonotidae, *Cu.* †*gigas* Théobald, 1937, from Early Oligocene shale from Les Camoins, Provence, France (Théobald 1937: 288) was re-examined by Kirk-Spriggs (2007), who concluded it was not Curtonotidae.

Identification

Unlike many of the Neotropical species of *Curtonotum sensu stricto*, which are strikingly marked, often with conspicuous picture wings and abdominal patterning, the Afrotropical species are by contrast more conservative and phenotypically very similar, frequently only distinguishable on slight, but consistent, differences in the male terminalia. Currently only males of the genus *Curtonotum sensu lato* and all genera formerly regarded as *Cyrtona* can be identified to species. Kirk-Spriggs (2008c), for example, undertook a qualitative assessment of intra- and interspecific variability in the spermathecal structure of the *Curtonotum cuthbertsoni* complex (*sensu* Tsacas 1977), to assess their value in species-level identification and concluded that these were far too variable to be of any value in distinguishing species. Likewise, females of *Cyrtona* cannot be associated with males on external characters, but this may be possible in the future by use of genetic barcodes. Until such time as that is done, female spermathecae cannot be fully assessed and used as characters in a phylogeny.

The genus "*Cyrtona*" has never been properly diagnosed and the only character used to define the group is the absence of discal scutellar setae. As currently recognised, the genus comprises several genera, but these cannot be formally described until generic limits are properly defined and all genera are included in a phylogeny. For this reason, the below key (which should work for both males and females), should be regarded as preliminary until a more complete generic review is published. It is worth noting that all three undescribed genera listed below (plus the now described genus *Tigrisomyia*), were also regarded as undescribed genera by L. Tsacas, who flagged them as such on written notes appended to museum specimens. Species identification of all Afrotropical Curtonotidae requires dissection and careful examination of the male terminalia. Curtonotidae are best micro-pinned in the field for later double-mounting (see Chapter 2).

Key to genera of Afrotropical Curtonotidae

1. Scutellar disk setose, at least in anterior ½ (e.g., Figs 45, 46, 51). 2
– Scutellar disk entirely bare (e.g., Figs 47–50, 52, 53) 5

2. Costal wing vein (C) with large conspicuous costal spines in basal ⅔ (e.g., Figs 72, 74); wing either pointed with membrane largely darkly infuscate (e.g., Fig. 72), or evenly rounded and faintly grey to pale brown, darker over *r–m* and *dm–m* crossveins (e.g., Fig. 74) 3

– Costal wing vein (C) without large conspicuous costal spines in basal ⅔ (e.g., Figs 73, 83); wing either pointed with membrane entirely hyaline (e.g., Fig. 73) or evenly rounded with diffuse pattern of brown in apical ½ and over *r–m* and *dm–m* crossveins (e.g., Fig. 83). 4

3. Head with proclinate fronto-orbital seta greatly reduced (microscopic) (Fig. 9); scutum with extreme hunchbacked appearance (Figs 65, 68); head partly tucked below thorax viewed from above (Fig. 45); scutum dark brown with two pairs of narrow paler dorsocentral vittae (Figs 45, 68); wing with pointed apex (Fig. 72); veins and membrane darkly infuscate, especially in cells r_1 and r_{2+3} (Fig. 72); abdomen with maculae as illustrated in Figs 86, 87; male terminalia with epandrium and hypandrium fused and surstylus bifurcate (Fig. 91); ejaculatory apodeme internal within phallapodeme (Fig. 92); female spermatheca barrel-shaped (Figs 153, 154) (*A. fuscipennis* species-group) . . . . . *Axinota* Wulp [in part]

– Head with proclinate fronto-orbital seta well-developed, over ½ length of posterior reclinate fronto-orbital seta (Figs 6, 10); scutum with moderate hunchbacked appearance (Figs 3, 66, 67), head not partly tucked below thorax viewed from above (Fig. 46); scutum pale brown/grey to straw yellow, with two pairs of wider brown dorsocentral vitta (Figs 3, 46); wing apex evenly rounded (Fig. 74); membrane grey to pale brown, darker over *r–m* and *dm–m* crossveins (Figs 74); abdomen with row of elliptical black maculae laterally (*Curtonotum striatifrons* species-group) (Fig. 67) or "T-shaped" lateral maculae, developed to a greater (Fig. 66) or lesser degree (Fig. 3); male terminalia with epandrium and hypandrium separate, surstylus not bifurcate (Figs 95, 98, 100, 103, 106, 109); ejaculatory apodeme external on phallapodeme (Figs 96, 99, 101, 104, 107, 110); female spermathecae either elongate with studded or wrinkled surface (Figs 156–158) or tear-shaped with wrinkled surface (Figs 159–161) . . . . . .*Curtonotum* Macquart *sensu lato*

4. Head without proclinate fronto-orbital seta; scutum with extreme hunchbacked appearance (head partly tucked below thorax viewed from above) (Fig. 2), ground colour pale brown, with greyish white to blue pruinescent and distinct dorsocentral vittae (Fig. 2); frons markedly narrowed in male (Kirk-Spriggs 2010*a*, fig. 3); wing with pointed apex, membrane entirely clear hyaline (Fig, 73); scutellum with basomedial macula (Kirk-Spriggs 2010*a*, figs 11, 12); male terminalia with surstylus bifurcate (Fig. 93); ejaculatory apodeme internal (Fig. 94) (*A. pictiventris* species-group) . . . . . *Axinota* Wulp [in part]

– Head with well-developed proclinate fronto-orbital seta, over ½ length of posterior reclinate fronto-orbital seta (Fig. 15); scutum with moderate hunchbacked appearance (head not partly tucked below thorax) (Figs 42, 51), ground colour uniformly dark chestnut brown, without dorsocentral vittae (Fig. 51); frons not markedly narrowed in male (Fig. 15); wing tip evenly rounded, with membrane diffusely darkened in apical ½ and over *r–m* and *dm–m* crossveins (Fig. 83); scutellum concolourous with scutum, without basomedial macula (Fig. 51); male terminalia with surstylus subdivided, but not bifurcate (Fig. 128); ejaculatory apodeme external (Fig. 129) . . . . . Undescribed genus B

5. Head with frons black to brown, extensively yellow in anterior ½, surface pitted, but sub-shiny (Figs 5, 17, 25); thorax strikingly marked with silver-dusted triangular macula anterior to transverse suture laterally, with dark macula posterior to transverse suture and dark fascia at anterior margin (Figs 5, 53, 69–71); wing relatively narrow, evenly rounded to bluntly pointed, faintly infuscate yellow throughout (Fig. 85); abdomen yellow with black fasciae or yellow maculae laterally (Figs 5, 53); male terminalia with cercus grossly extended posteriorly with 4–5 enormously long, wavy apical setae; surstylus spatulate, with apical notch or indentation (Fig. 132); phallus with basiphallus considerably lengthened, distiphallus with ventral process and dorsolaterally expanded projection; phallapodeme deeply incised basally (Fig. 133) . . . . . *Tigrisomyia* Kirk-Spriggs

– Head with frons predominately brown, not extensively yellow in anterior ½, without surface pitted (e.g., Figs 11–14, 16); thorax not strikingly marked with silver-dusted triangular macula (e.g., 47–50, 52); wing not narrow, evenly rounded, not faintly infuscate yellow throughout (e.g., Figs 75–82, 84); abdomen not with black fasciae or yellow maculae laterally (e.g., Figs 1, 4, 89, 90); male terminalia not as described above (e.g., Figs 112–127, 130, 131) 6

6. Wing membrane either distinctly maculate, with auxiliary vein from vein M_1 into cell *dm* (e.g., Figs 77–79), or wing unmarked, with anal lobe distinctly broadened (e.g., Fig. 84); scutum predominately grey, with distinct brown dorsocentral vittae (e.g., Figs 48, 52) 7

– Wing membrane either with diffuse darker marking in anterior ½ (in cells r_1, r_{2+3}, r_{4+5}), at base of cell r_1, over *dm–m* crossvein and along vein M_4 dorsally in cell m_1 (e.g., Fig. 82), or wing membrane grey/brown, darker over *r–m* and *dm–m* crossveins only (e.g., Figs 75, 76, 80, 81); scutum either with uniform pale brown ground colour and paler brown dorsocentral vittae (e.g., Fig. 50), or ground colour grey with blotchy yellow or brown markings (e.g., Figs 1, 4, 47, 49) 8

7. Wing distinctly maculate, with auxiliary vein on vein M_1 into cell *dm* (e.g., Figs 77–79); scutal setae with dark marks at bases around sockets (Figs 39, 48), central dorsocentral vittae extending onto scutellum (Fig. 48), or scutellum black-brown, with paler margins; head as illustrated in Figs 12, 20; antennal arista with long to medium length dorsal branches (Figs 27–29); abdomen either grey with darker central fascia and lateral maculae (Figs 89, 90), or black-brown with elongate paler maculae at posterior margins of tergites; male terminalia with surstylus not greatly enlarged and semicircular (Figs 116, 118, 120); phallus very long; phallapodeme long, with basal lobe; basiphallus foreshortened; distiphallus greatly lengthened more or less spatulate apically (Figs 117, 119, 121) . . . . . *Cyrtona* Séguy *sensu stricto*

– Wing membrane brownish, unmarked, with anal lobe distinctly broadened, without auxiliary vein on vein M_1 (Fig. 84); scutal setae without dark marks around bases of sockets (Figs 43, 52), central dorsocentral vittae not extending onto scutellum (Fig. 52); head as illustrated in Figs 16, 24; antennal arista short-haired (Fig. 24); abdomen not as described above; male terminalia with surstylus greatly enlarge, semicircular (clearly visible in undissected males) (Fig. 130); phallus greatly reduced in size and foreshortened, with phallapodeme sub-triangular; basiphallus length sub-equal to length of phallapodeme (Fig. 131) . . . . . Undescribed genus C

8. Wing membrane with diffuse darker marking in discal ½ (in cells r_1, r_{2+3}, r_{4+5}), at base of cell r_1, over *dm–m* crossvein and along vein M_4 dorsally in cell m_1 (Fig. 82); scutum with uniform pale brown ground colour and paler brown dorsocentral vittae (Fig. 50); head as illustrated in Figs 14, 22; subscutellum large, wide and bulging (Fig. 63); abdomen not as described below; male terminalia greatly reduced in size (Figs 126, 127); phallus with phallapodeme triangular; phallic plate tapering ventrally; basiphallus subequal to sclerotised part of distiphallus (Fig. 127) . . . . . Undescribed genus A

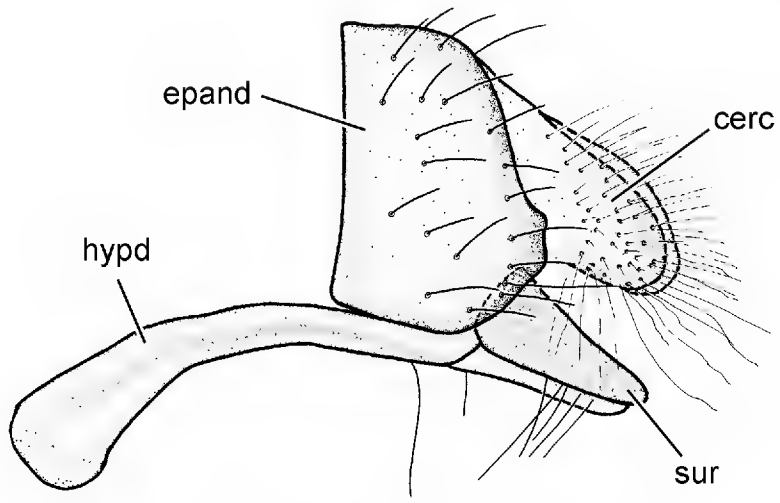
– Wing membrane grey/brown, darker over *r–m* and *dm–m* crossveins only (e.g., Figs 75, 76, 80, 81); scutum with ground colour grey with blotchy yellow or brown markings (e.g., Figs 1, 4, 47, 49); head as illustrated in Figs 11, 13, 19, 21; subscutellum not as described above (e.g., Figs 56, 57, 61, 62); abdomen either brown to black with 2 dorsal and 1 lateral rows of large, elliptical silver-white maculae (e.g., Fig. 4), or predominantly grey or grey with dark medial facia and lateral maculae (e.g., Fig. 1); male terminalia not reduced in size; not as described above (e.g., Figs 112–115, 122–125) 9

9. Abdomen brown to black, with 2 dorsal and 1 lateral rows of strongly contrasting large, elliptical silver-white maculae (lateral maculae sometimes merging) (e.g., Fig. 4); scutum distinctly darkly mottled, with pigmentation patches in regions of transverse suture and of lateral dorsocentral vitta (Figs 4, 49); anepisternum with two dark pigmentation patches at dorsal and ventral anterior margin (Fig. 40); head as illustrated in Figs 13, 21; male terminalia with distiphallus apically with distended and inflated membranous portion (Figs 123, 125) . . . . . *Cyrtona "Parapsinota"*

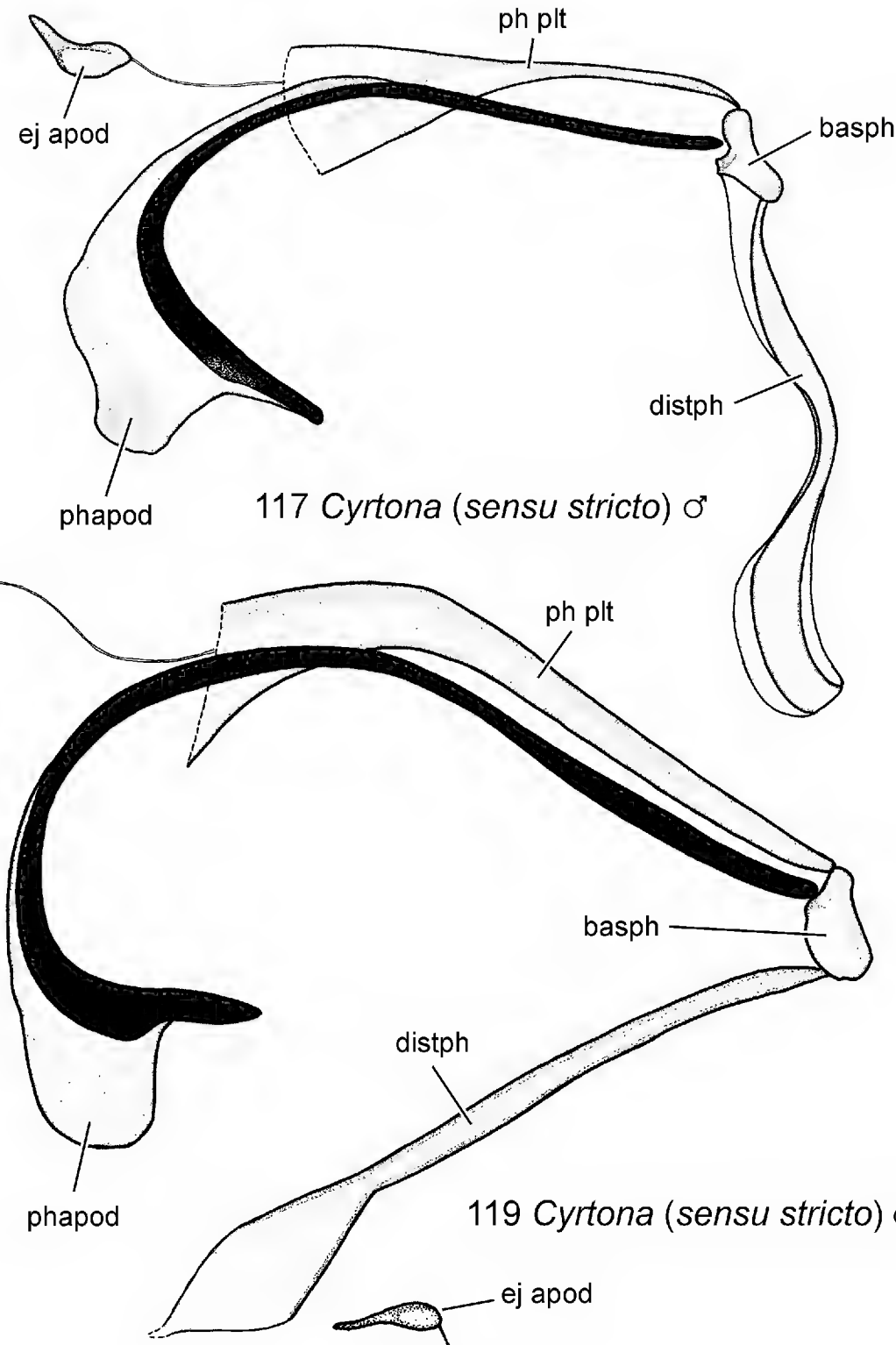
– Abdomen predominantly grey, or grey with dark medial facia and/or lateral maculae (e.g., Fig. 1); scutum not distinctly darkly mottled, sometimes with pigment patches in region of lateral dorsocentral vitta (Figs 1, 47); anepisternum unicolourous grey, or with paler yellow pigmentation patches (Figs 1, 38); head as illustrated in Figs 11, 19; male terminalia with distiphallus without apically distended and inflated membranous portion (Figs 113, 115) . . . . . *Cyrtona sensu lato*

Synopsis of the fauna

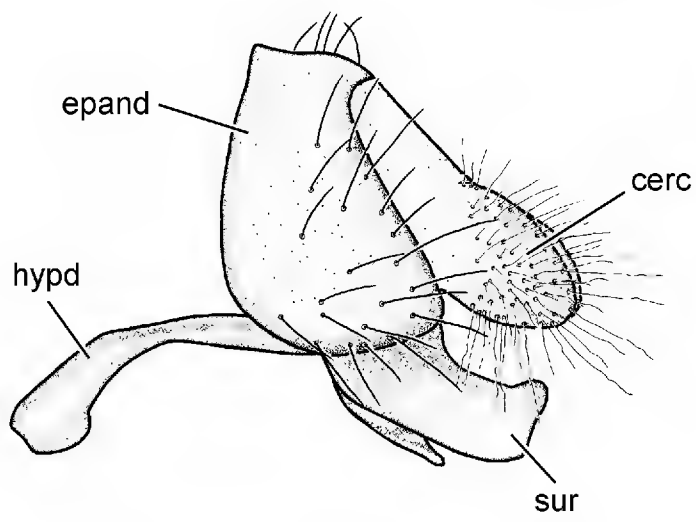
***Axinota* Wulp.** A genus of 12 described species (Figs 2, 65), occurring in the Afrotropical, Australasian/Oceanian and Oriental Regions (Kirk-Spriggs 2010*a*). The genus is primarily Oriental with four species recorded from the Afrotropics. No additional undescribed species are known. The genus is distinguished as follows: head either with one prominent posterior reclinate fronto-orbital seta and one tiny anterior reclinate fronto-orbital setula inserted close to the socket of the posterior fronto-orbital seta, or with an additional tiny proclinate fronto-orbital setula. The frons is narrow in the male or wide in both sexes. The scutum is of an extreme hunchbacked appearance. The wing membrane is dark brown infuscate throughout, or infuscate with a darker marginal band in cell r_1 and the anterior half of cell r_{2+3} or is entirely hyaline. The costal wing vein (C) has either a row of prominent semi-erect setae (Fig. 72), or a row of short, weak, semi-erect regular setae (Fig. 73) for two-thirds of the costal length from the costagial break. The scutellum has the intermediate scutellar setula weak or well-developed. The male terminalia has the epandrium and hypandrium either free (Fig. 93) or fused (Fig. 91) and has the surstylus distinctly forked apically (Figs 91, 93) and the female spermatheca is globular, mushroom- or barrel-shaped (Figs 153–155). Kirk-Spriggs (2010*a*) divided the genus into the largely Oriental *A. pictiventris* species-group (Fig. 2), with the wing entirely clear hyaline and with short regular spines on the costal vein (Fig. 73) and the endemic *A. fuscipennis* species-group (Fig. 65), with the wing infuscate and the costal vein with a row of prominent semi-erect spines (Fig. 72). The former species-group includes two Afrotropical species: *A. ahdabi* Kirk-Spriggs, 2010, described from Yemen in the Southern Arabian Peninsula and *A. kyphosis*, confined to Madagascar. The latter species-group comprises two widely distributed species confined to the continental Afrotropics: *A. fuscipennis* (Macquart, 1844) and *A. quasimodoi* Kirk-Spriggs, 2010. Biology and immature stages remain unknown. Kirk-Spriggs (2010*a*) mapped the distribution of the four Afrotropical species (figs 29, 30) and discussed biogeographical implications, noting that the *A. fuscipennis* species-group appear to be



116 *Cyrtona* (*sensu stricto*) ♂

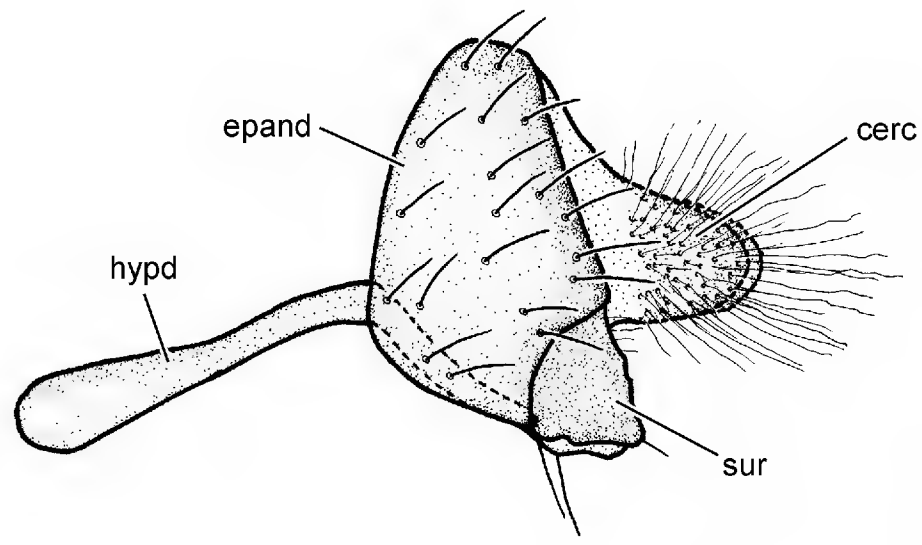


117 *Cyrtona* (*sensu stricto*) ♂

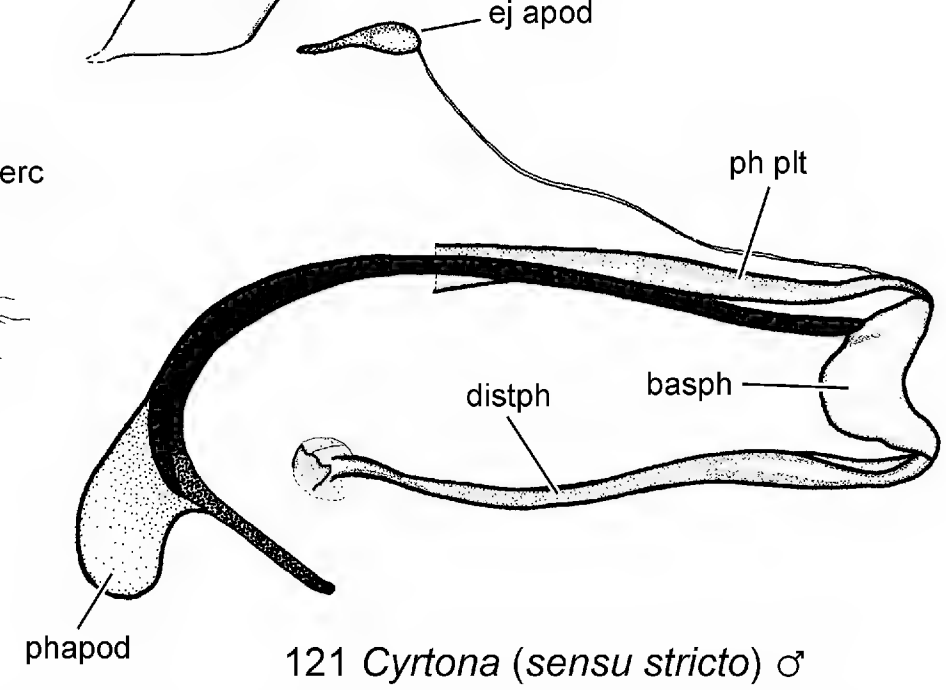


118 *Cyrtona* (*sensu stricto*) ♂

119 *Cyrtona* (*sensu stricto*) ♂



120 *Cyrtona* (*sensu stricto*) ♂



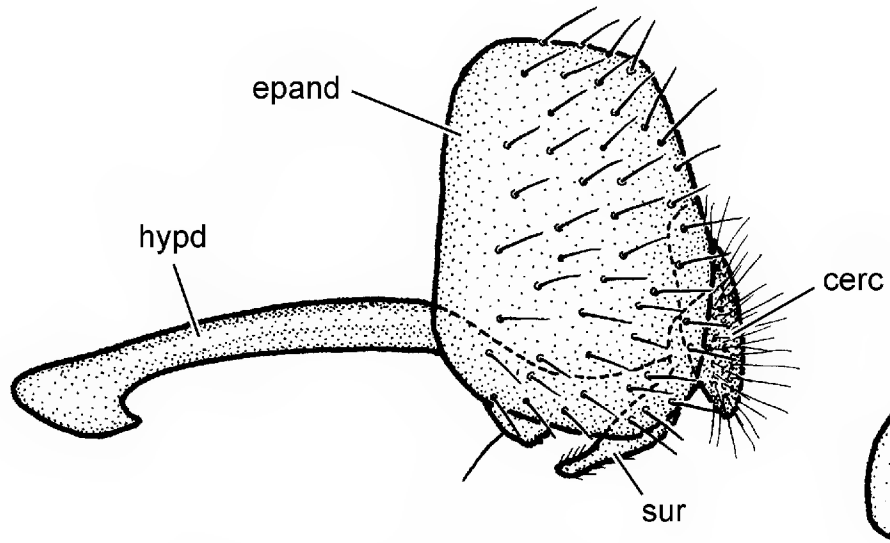
121 *Cyrtona* (*sensu stricto*) ♂

Figs 103.116–121. Male terminalia of Curtonotidae (lateral views): (116) epandrium and hypandrium of *Cyrtona* (*s.s.*) *appendiculata* Séguy; (117) same, phallus, right lateral view; (118) epandrium and hypandrium of *Cy.* (*s.s.*) *pictipennis* (Thomson); (119) same, phallus, right lateral view; (120) epandrium and hypandrium of *Cyrtona* (*s.s.*) sp.; (121) same, phallus, right lateral view. Figs 116–121 (Kirk-Spriggs & Wiegmann 2013, figs 56, 59, 57, 60, 61, 64, respectively © Magnolia Press).

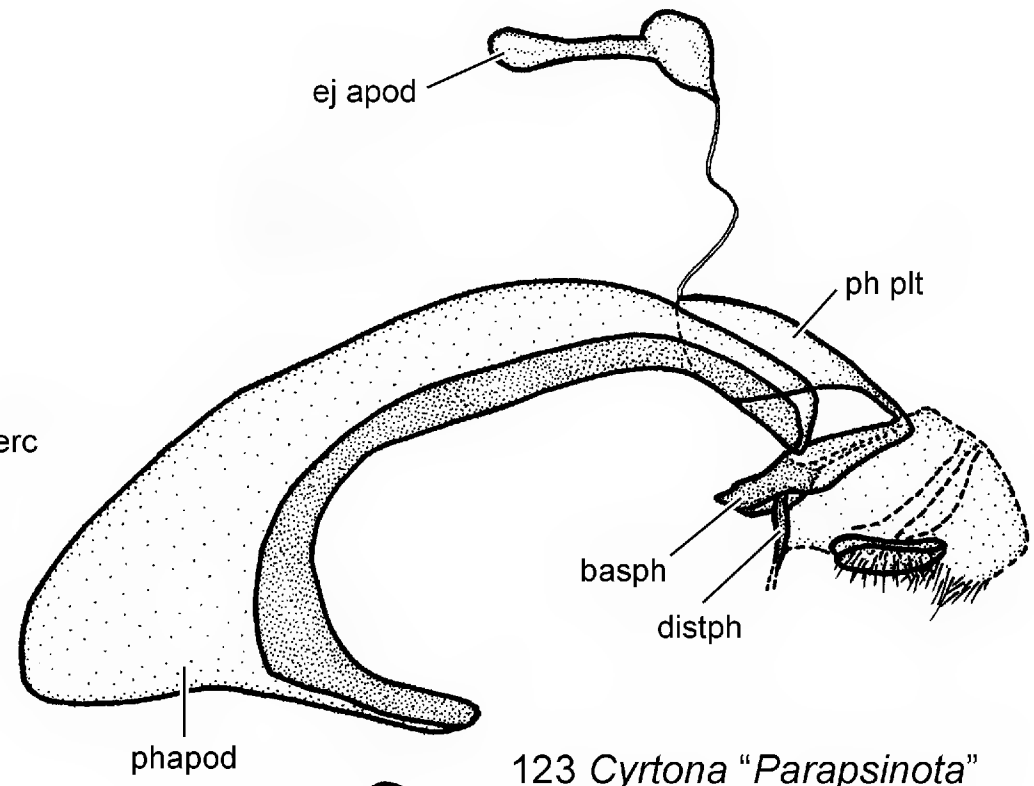
Abbreviations: basph – basiphallus; cerc – cercus; distph – distiphallus; ej apod – ejaculatory apodeme; epand – epandrium; hypd – hypandrium; ph plt – phallic plate; phapod – phallapodeme; sur – surstylus.

primarily associated with gallery forest. Afrotropical species of the genus were revised by Kirk-Spriggs (2010*a*), who provided an identification key.

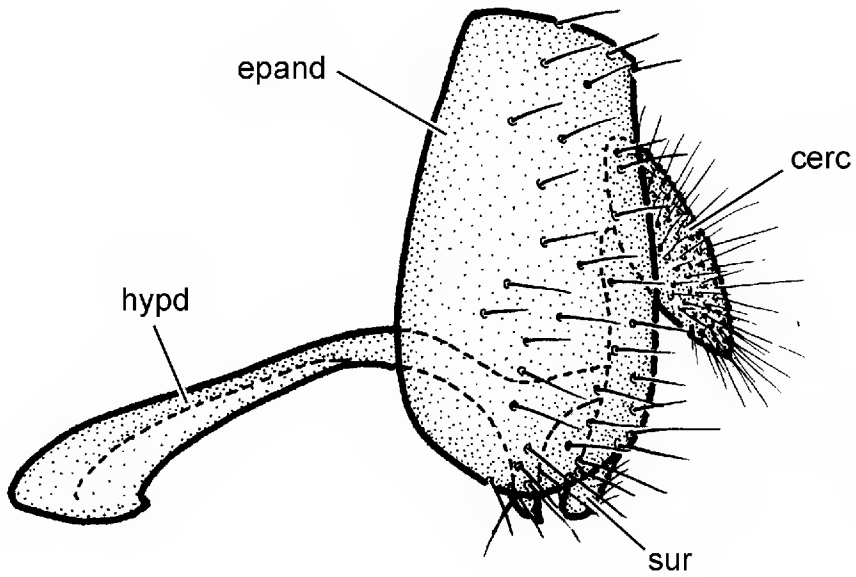
***Curtonotum* Macquart (*sensu lato*).** A genus of 81 described species occurring in all zoogeographical regions except the Australasian/Oceania Region and Antarctica (Afrotropical: 37 species, Neotropical: 35, Palaearctic: 4, Oriental: 3 and Nearctic: 2 (Kirk-Spriggs & Wiegmann 2013; Lindsay *et al*. 2019; Mello & Pereira-Colavite 2018)). As currently defined, *Curtonotum* is the largest and most widely distributed genus of the family and the only genus in the New World. Klymko & Marshall (2011), however, suggested restricting the name *Curtonotum* to a clade of Neotropical species and that clade is here regarded as *Curtonotum sensu stricto*. Only two species are recorded from more than one zoogeographical region, the predominantly Palaearctic *Cu. anus* (Meigen, 1830), which extends eastwards into Pakistan in the Oriental Region and the predominantly Afrotropical *Cu. simile*, which extends north-eastwards into Israel in the Palaearctic and also into Oman, United Arab Emirates and



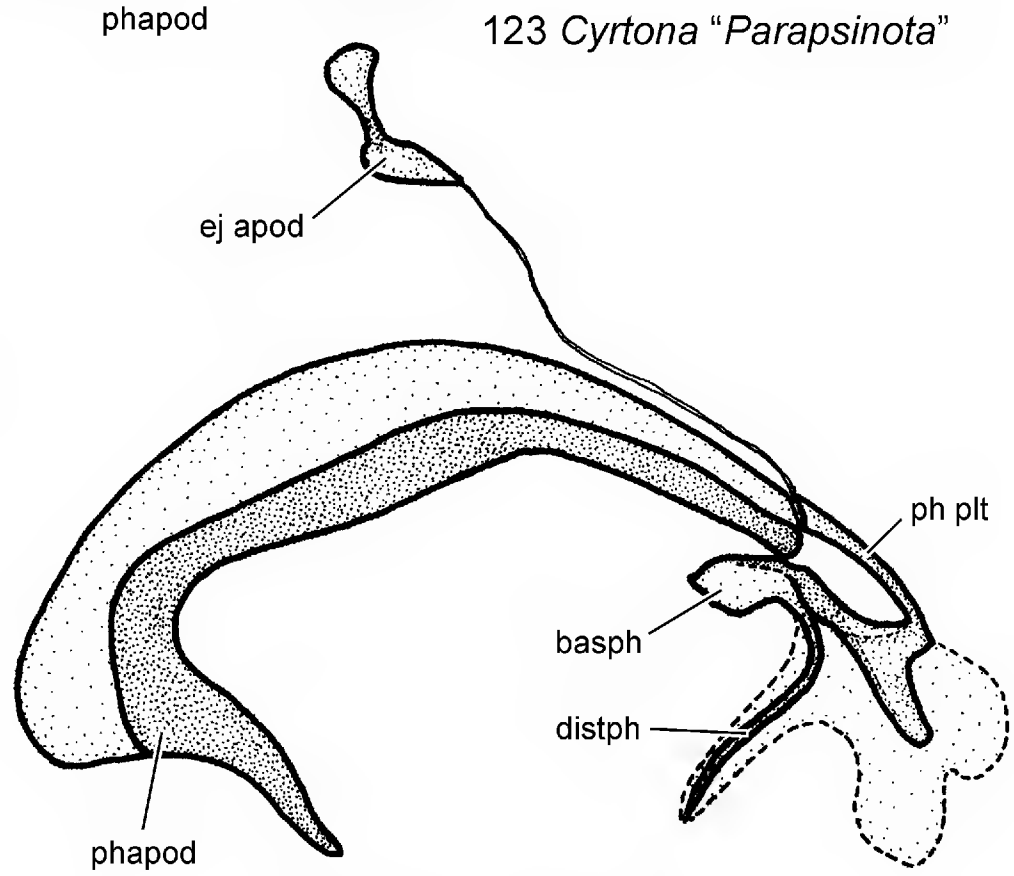
122 *Cyrtona* "*Parapsinota*"



123 *Cyrtona* "*Parapsinota*"



124 *Cyrtona* "*Parapsinota*"

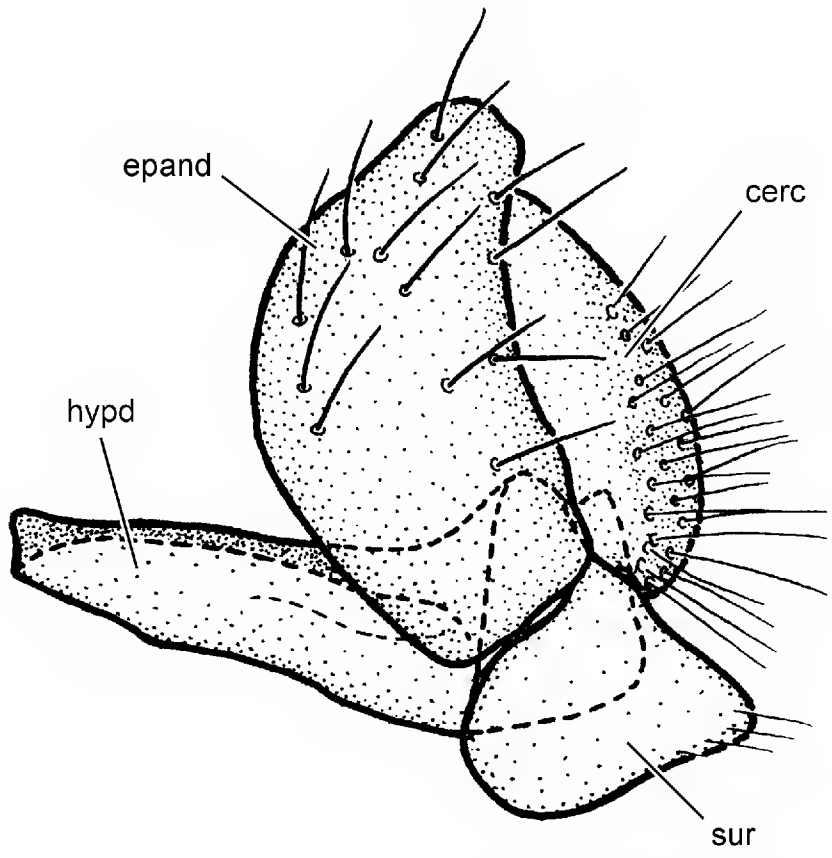


125 *Cyrtona* "*Parapsinota*"

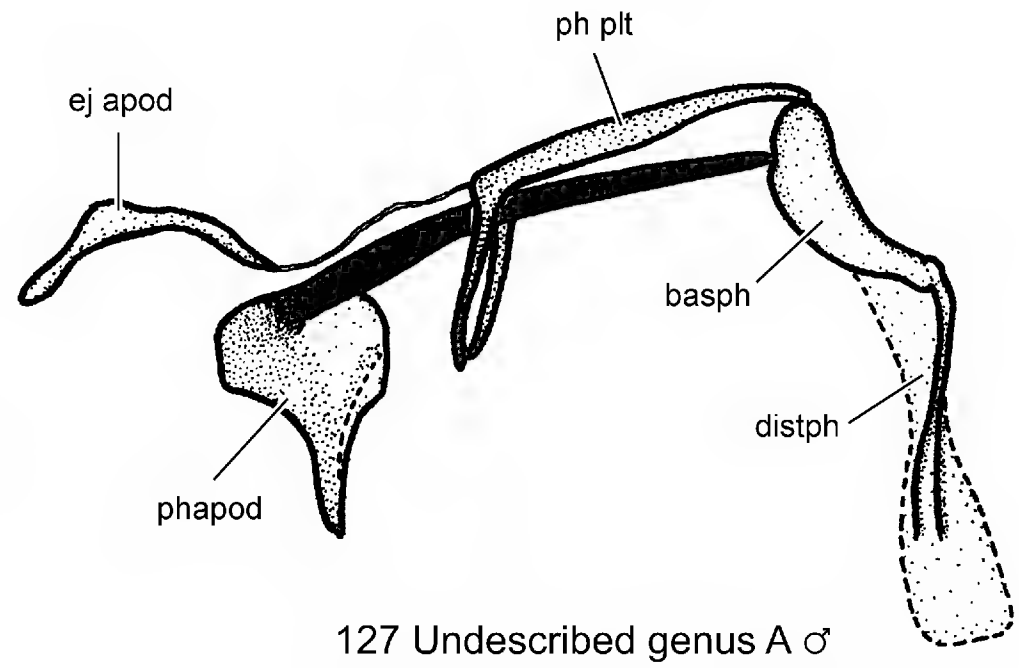
Figs 103.122–125. Male terminalia of Curtonotidae (lateral views): (122) epandrium and hypandrium of *Cyrtona "Parapsinota" albomacula* (Curran); (123) same, phallus, right lateral view; (124) epandrium and hypandrium of *Cy. "Parapsinota" sublineata* Duda; (125) same, phallus, right lateral view. Figs 122–125 (Kirk-Spriggs & Wiegmann 2013, figs 68–72 © Magnolia Press).

Abbreviations: basph – basiphallus; cerc – cercus; distph – distiphallus; ej apod – ejaculatory apodeme; epand – epandrium; hypd – hypandrium; ph plt – phallic plate; phapod – phallapodeme; sur – surstylus.

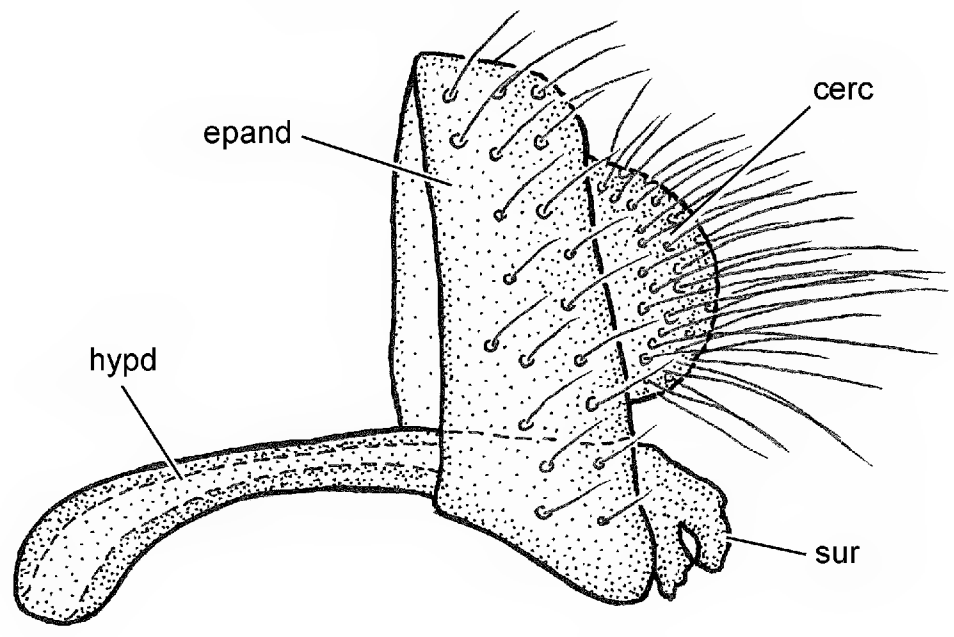
Yemen in the Afrotropical parts of the Southern Arabian Peninsula (Kirk-Spriggs & Freidberg 2007). The Malagasy fauna of the genus was first revised by Tsacas (1974) and more recently by Kirk-Spriggs (2011). Thirteen species are known from Madagascar, divided into three informal species-groups (Kirk-Spriggs & Wiegmann 2013), 12 of which are endemic to the island, with only *Cu. pauliani* Tsacas, 1974, occurring more widely in the continental Afrotropics (Namibia and South Africa). The genus is not recorded from any other Indian or Atlantic oceanic islands (Kirk-Spriggs 2011; Kirk-Spriggs & Wiegmann 2013), but it is likely that additional undescribed species will still be discovered in Madagascar. The continental Afrotropical species were first revised by Tsacas (1977) and more recently by Kirk-Spriggs & Wiegmann (2013). Twenty-five species are now recorded from the continental Afrotropics, divided into six informal species-groups. In the Afrotropical Region, species of the genus occur in a range of habitat types and biomes, including desert; semi-desert; wooded steppe, arid and mesic savannas; tropical forest margins; tropical grasslands; coastal forests; and mid- to high-elevation montane forest. Some species are restricted to



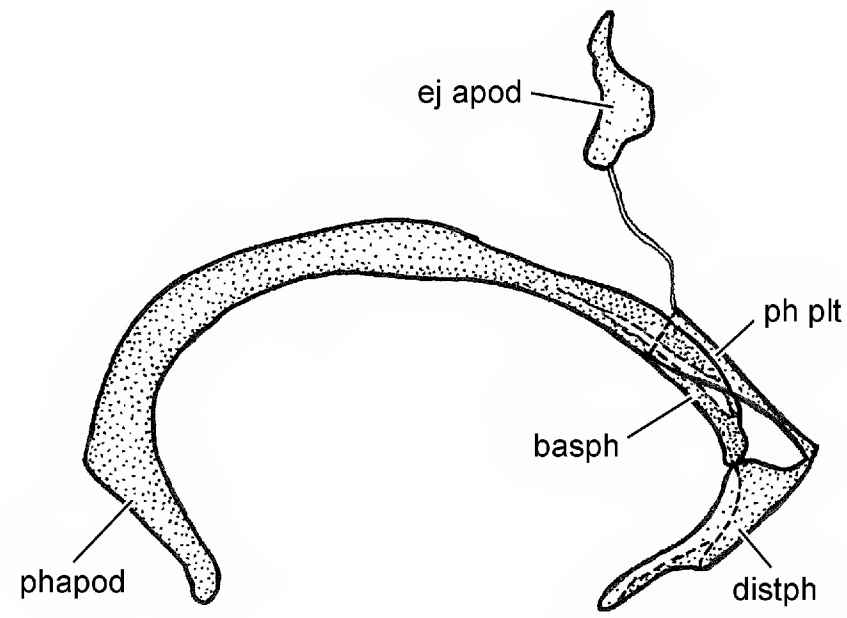
126 Undescribed genus A ♂



127 Undescribed genus A ♂



128 Undescribed genus B ♂



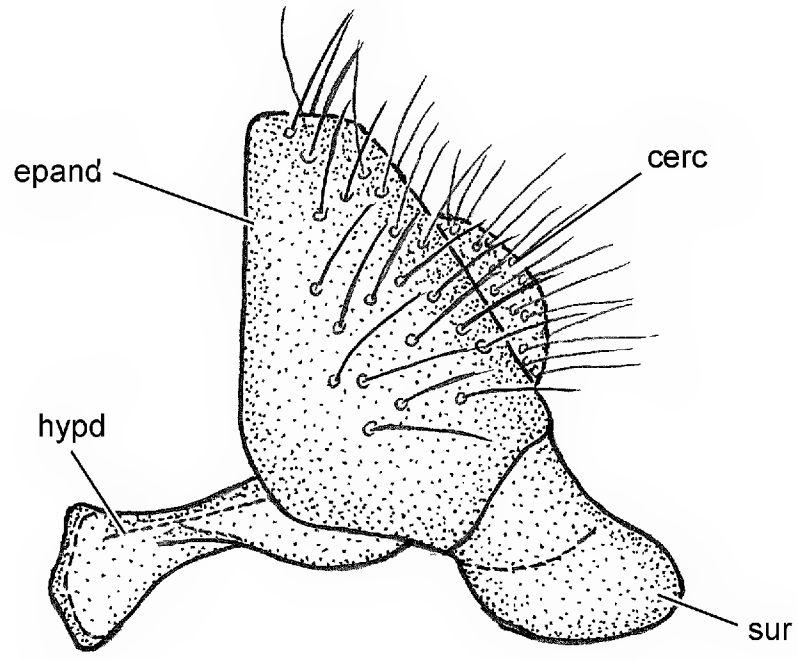
129 Undescribed genus B ♂

Figs 103.126–129. Male terminalia of Curtonotidae (lateral views): (126) epandrium and hypandrium of Undescribed genus A; (127) same, phallus, right lateral view; (128) epandrium and hypandrium of Undescribed genus B; (129) same, phallus, right lateral view. Figs 126, 127 (Kirk-Spriggs & Wiegmann 2013, figs 62, 65 © Magnolia Press).

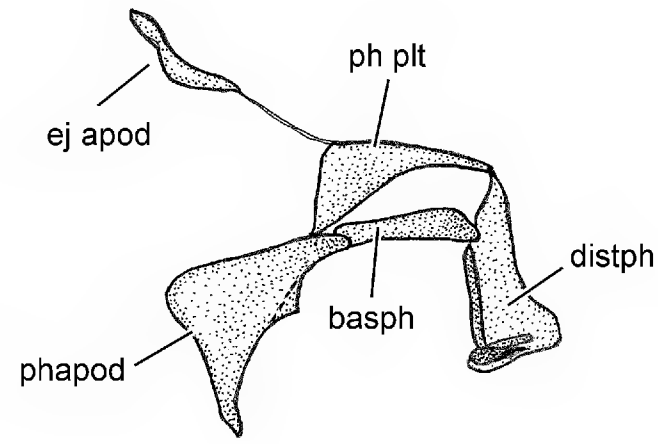
Abbreviations: basph – basiphallus; cerc – cercus; distph – distiphallus; ej apod – ejaculatory apodeme; epand – epandrium; hypd – hypandrium; ph plt – phallic plate; phapod – phallapodeme; sur – surstylus.

the Southern African Great Escarpment or East African Rift Valley or to isolated mountain ranges. The immature stages were most recently reviewed by Kirk-Spriggs (2008*b*). A key to the Malagasy species was provided by Kirk-Spriggs (2011) and to the continental Afrotropical species by Kirk-Spriggs & Wiegmann (2013).

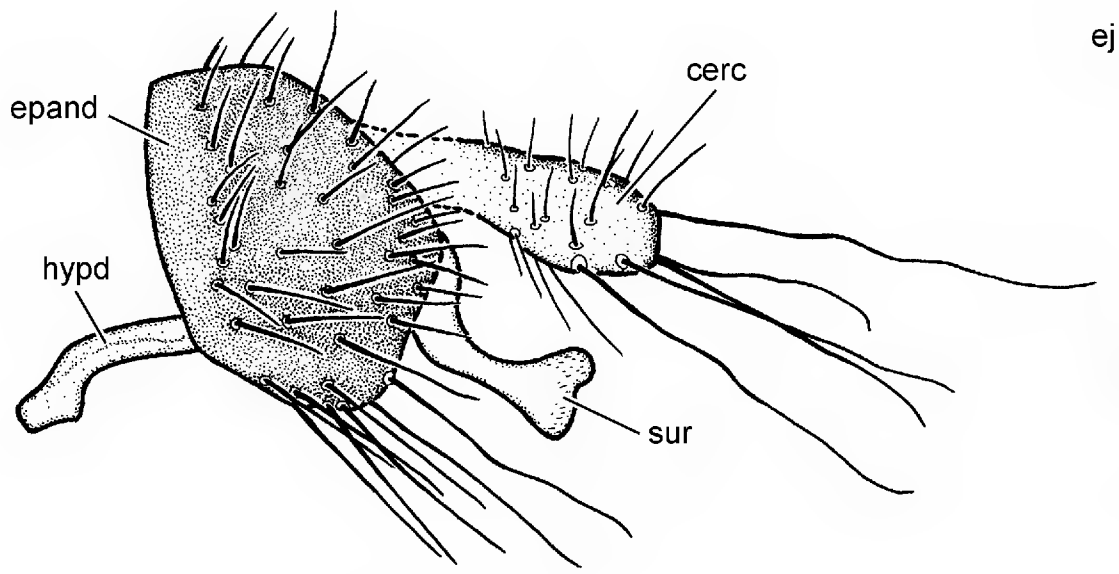
***Cyrtona* Séguy (*sensu stricto*).** An endemic genus of two described species. The genus *Cyrtona* has never been properly diagnosed and the only character used in the past to distinguish it from *Axinota* and *Curtonotum* was the bare scutellar disk. Currently, *Cyrtona sensu lato* includes six described species, only two of which are here regarded as *Cyrtona sensu stricto*, namely: *Cy. appendiculata* Séguy, 1938, described from Kenya, but with additional material examined from Democratic Republic of Congo, Malawi and Tanzania and *Cy. pictipennis* Thomson, 1869, described from South Africa, with additional material examined from Lesotho and Zimbabwe (Kirk-Spriggs, in prep.). Two undescribed species are known from South Africa and a third undescribed species from South Africa (referred to a *Cyrtona* (*s.s.*) sp. in the text and illustrated in Figs 29, 60, 79, 120, 121, 143, 165), is tentatively regarded as belonging to this genus pending a revision of the picture-winged species (Kirk-Spriggs, in prep.). The remaining four species currently ascribed to *Cyrtona* are dealt with under other generic headings. As here defined, *Cyrtona sensu stricto* is recognised by the very



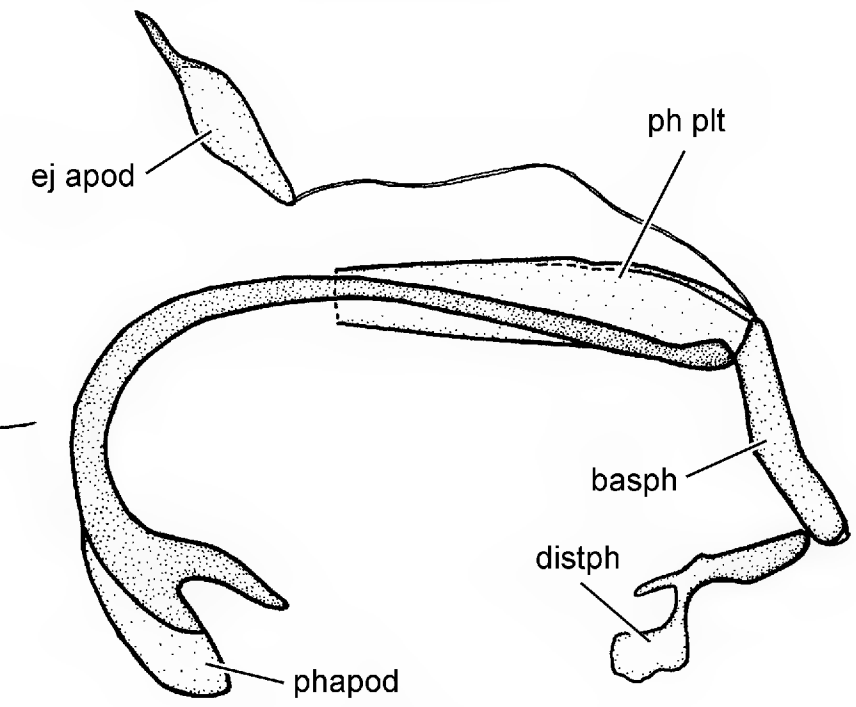
130 Undescribed genus C ♂



131 Undescribed genus C ♂



132 *Tigrisomyia* ♂



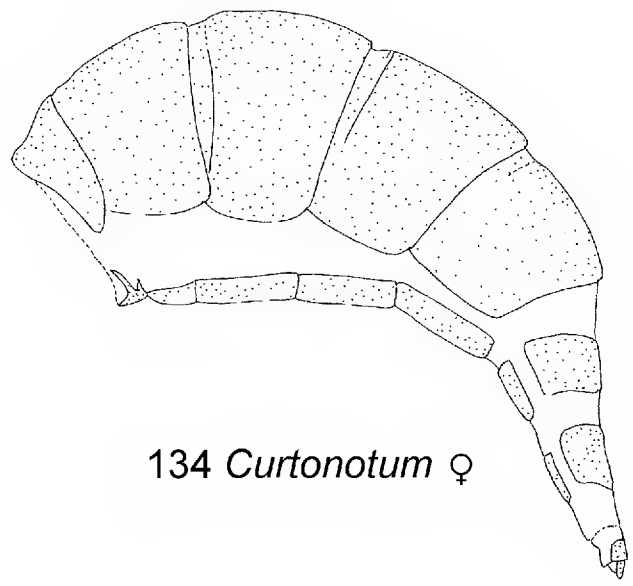
133 *Tigrisomyia* ♂

Figs 103.130–133. Male terminalia of Curtonotidae (lateral views): (130) epandrium and hypandrium of Undescribed genus C; (131) same, phallus, right lateral view; (132) epandrium and hypandrium of *Tigrisomyia amnoni* Kirk-Spriggs; (133) same, phallus, right lateral view. Figs 132, 133 (Kirk-Spriggs 2010*b*, figs 11, 14).

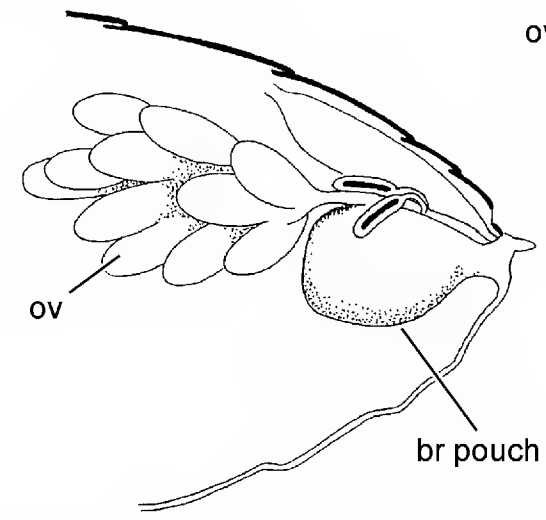
Abbreviations: basph – basiphallus; cerc – cercus; distph – distiphallus; ej apod – ejaculatory apodeme; epand – epandrium; hypd – hypandrium; ph plt – phallic plate; phapod – phallapodeme; sur – surstylus.

broad or pointed and strikingly patterned wing, with an auxiliary vein on vein M_1 extending into cell *dm* (Figs 77–79). The scutal setae have dark marks at their bases around the sockets (Figs 39, 48). The central dorsocentral vittae extend onto the scutellum (Fig. 48), or the scutellum is black-brown, with paler margins. The abdomen is either grey with a darker central fascia and lateral maculae (Figs 89, 90), or black-brown with elongate paler maculae at the posterior margins of the tergites and by the structure of the male terminalia (Figs 116–121). Species of *Cyrtona sensu stricto* appear to be chiefly associated with upland grassland habitats of the scarp mountains and Great Rift Valley of East and Southern Africa. The biology and immature stages remain unknown. The genus requires revision and no identification key to species is currently available.

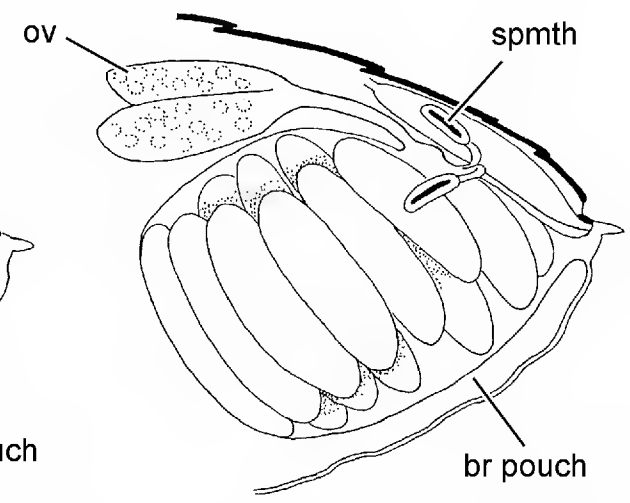
***Cyrtona "Parapsinota* Duda".** An undescribed genus of four described species (Fig. 4), occurring in the Afrotropical and Oriental Regions. Two species *Cyrtona albomacula* (Curran, 1933) and *Parapsinota sublineata* Duda, 1939 (as a variety of *Cy. angustipennis* (de Meijere, 1911)), belong in a genus of their own, with the latter species previously treated as *Parapsinota* Duda by Kirk-Spriggs & Wiegmann (2013). *Parapsinota* Duda is currently treated as a junior synonym of *Cyrtona*, but *Parapsinota* should be formally reinstated to include these two species, the two Oriental species *Curtonotum neoangustipennis* Dwivedi & Gupta, 1979 and *Cyrtona angustipennis* (de Meijere, 1911) and at least 15 undescribed species are known from the Afrotropical Region (Kirk-Spriggs, in prep.). The *Cyrtona "Parapsinota"* is widely distributed in the continental Afrotropics, but is absent from the Atlantic and Indian oceanic islands, including Madagascar. It includes some very widely distributed and common species in the Afrotropics and some species confined to mountain ranges and remnant forest habitats. At this time species can only be delimited on the structure of the male terminalia (e.g., Figs 122–125). As here defined, the genus is recognised by the brown to black abdomen with two dorsal and one lateral rows of strongly contrasting large, elliptical silver-white maculae (the lateral maculae sometimes merging) (Fig. 4). The scutum is distinctly darkly mottled, with pigmentation patches in the regions of the transverse suture and the lateral dorsocentral vitta (Figs



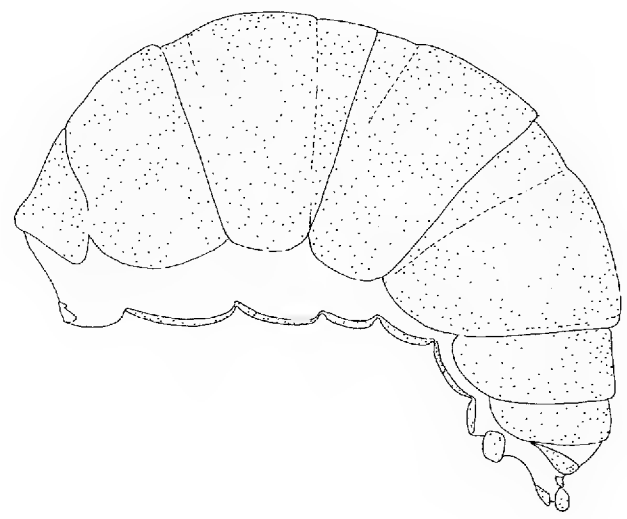
134 *Curtonotum* ♀



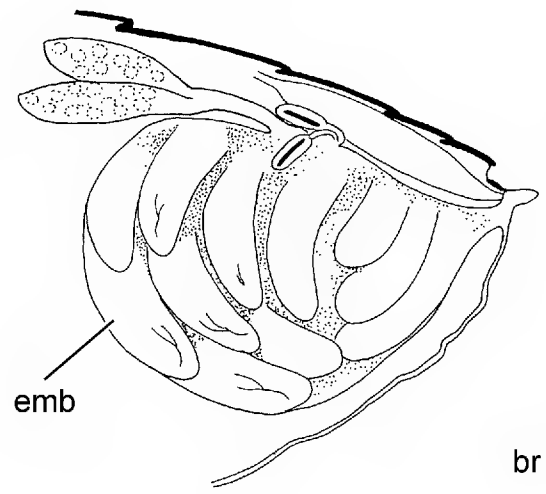
136 *Cyrtona* "*Parapsinota*" ♀



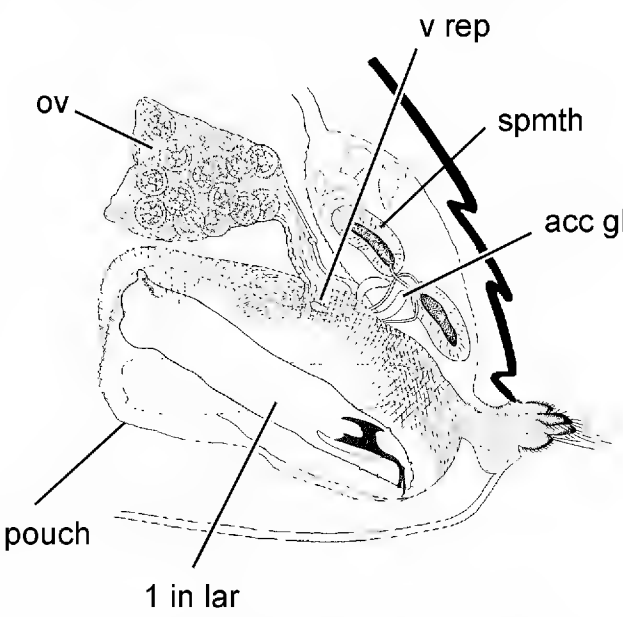
138 *Cyrtona* "*Parapsinota*" ♀



135 *Cyrtona* "*Parapsinota*" ♀



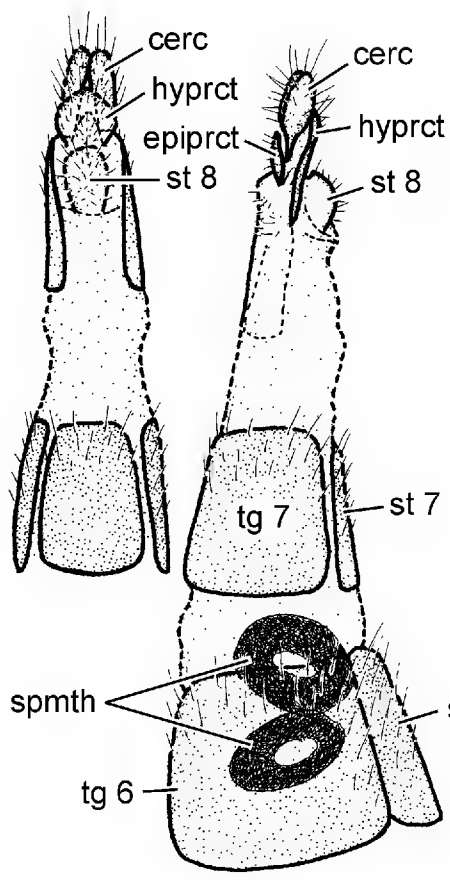
137 *Cyrtona* "*Parapsinota*" ♀



139 *Cyrtona* "*Parapsinota*" ♀

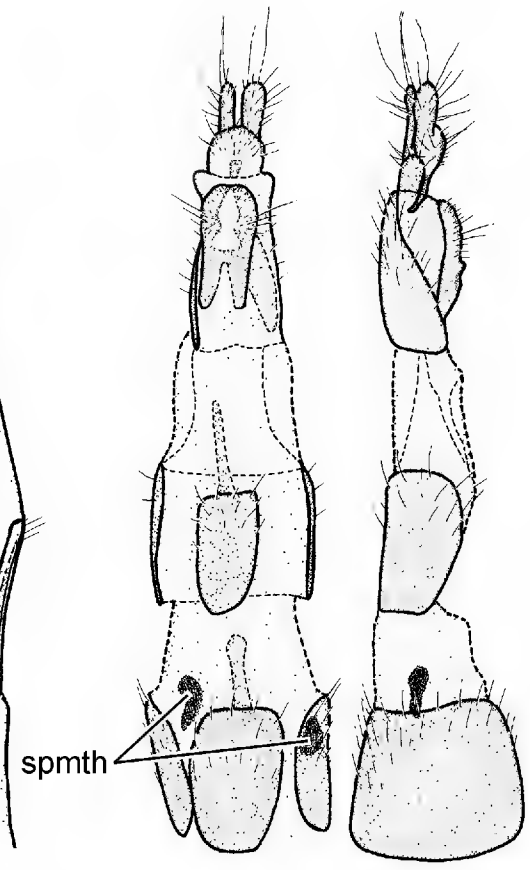
Figs 103.134–139. Female abdomens and reproductive system of Curtonotidae: (134) abdomen of *Curtonotum quinquevittatum* Curran, lateral view (oviparous); (135) same, *Cyrtona "Parapsinota"* sp. (multilarviparous); (136) female reproductive system of multilarviparous *Cyrtona "Parapsinota"* sp., with partially developed eggs in ovaries; (137) same, eggs passed into brood pouch and ovaries exhausted; (138) same, developing embryos within brood pouch; (139) same, abdomen with first-instar larva within brood pouch. Figs 134, 135 (after Pollock 2002, figs 9a, b), Figs 136–139 (after Pollock 1996, figs 2, 3).

Abbreviations: 1 in lar – first-instar larva; acc gl – accessory gland; br pouch – brood pouch; emb – embryo; ov – ovariole; spmth – spermatheca; v rep – ventral receptacle.

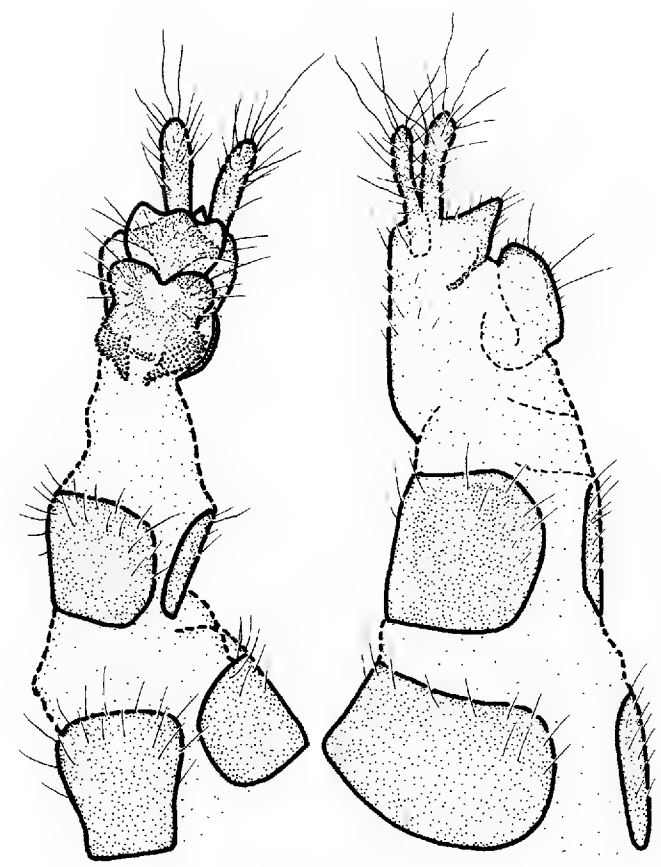


140 *Axinota* ♀

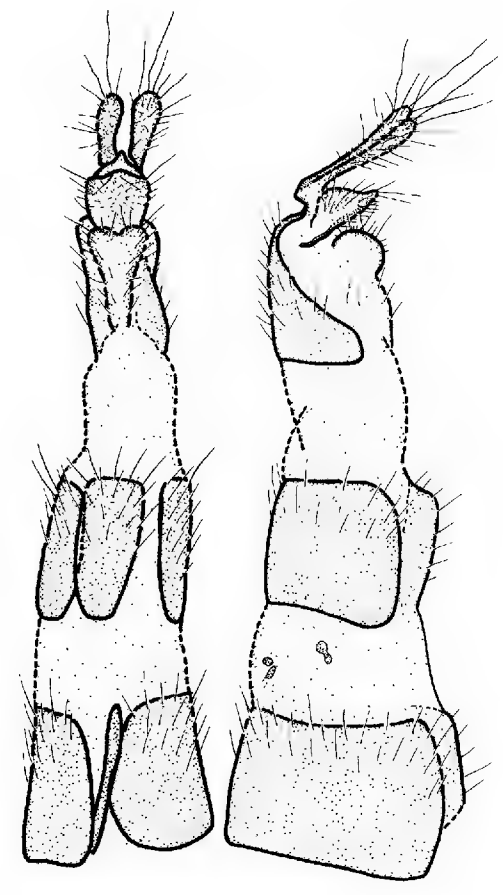
141 *Tigrisomyia* ♀



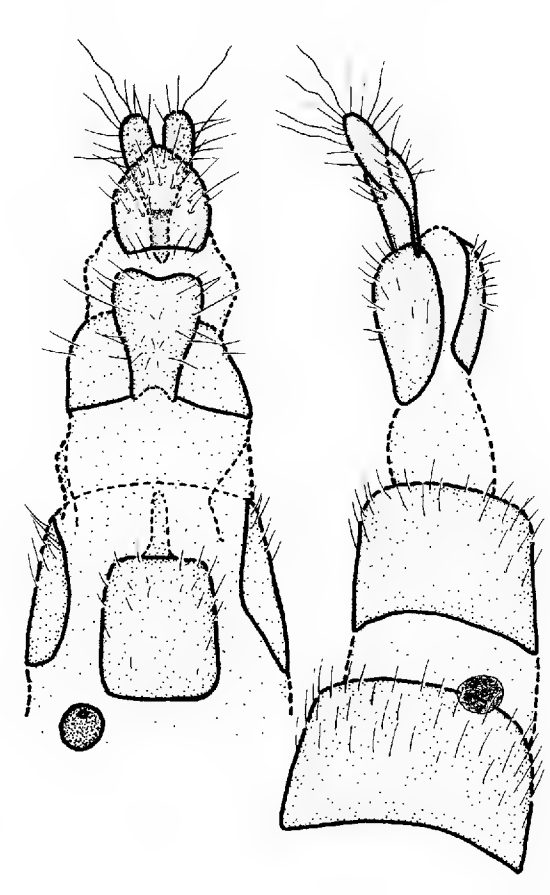
142 *Cyrtona* (*sensu stricto*) ♀



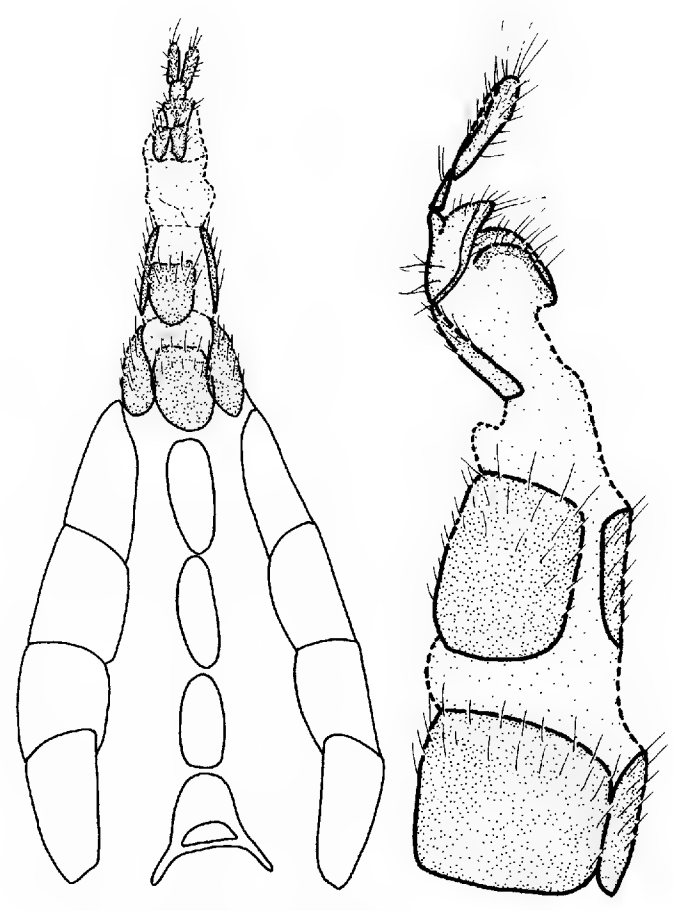
143 *Cyrtona* (*sensu stricto*) ♀



144 Undescribed genus A ♀



145 *Cyrtona* (*sensu lato*) ♀



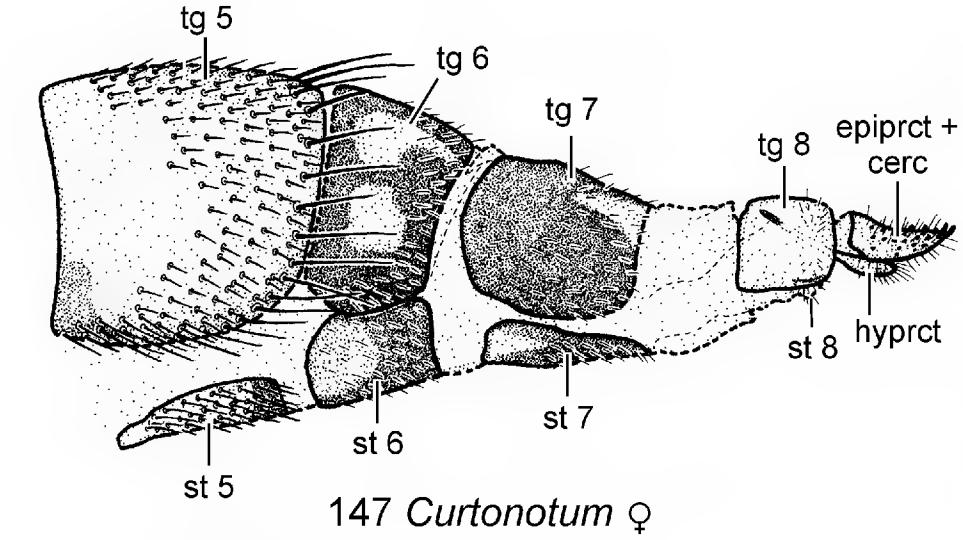
146 *Cyrtona* "*Parapsinota*" ♀

Figs 103.140–146. Female postabdomens of Curtonotidae: (140) *Axinota dissimilis* (Malloch), ventral view (left), lateral view (right) (non-Afrotropical); (141) *Tigrisomyia amnoni* Kirk-Spriggs, ventral view; (142) *Cyrtona* (*s.s.*) *appendiculata* Séguy, ventral view (left), lateral view (right); (143) *Cy.* (*s.s.*) sp., ventral, view (left), lateral view (right); (144) Undescribed genus A, ventral view (left), lateral view (right); (145) *Cy.* (*s.l.*) *capensis* Hackman, ventral view (left), lateral view (right); (146) *Cyrtona "Parapsinota"* sp. (oviparous), whole abdomen, ventral view (setation omitted on segments 1–5) (left), lateral view (right). Figs 140–146 (Kirk-Spriggs & Wiegmann 2013, figs 87–99 © Magnolia Press).

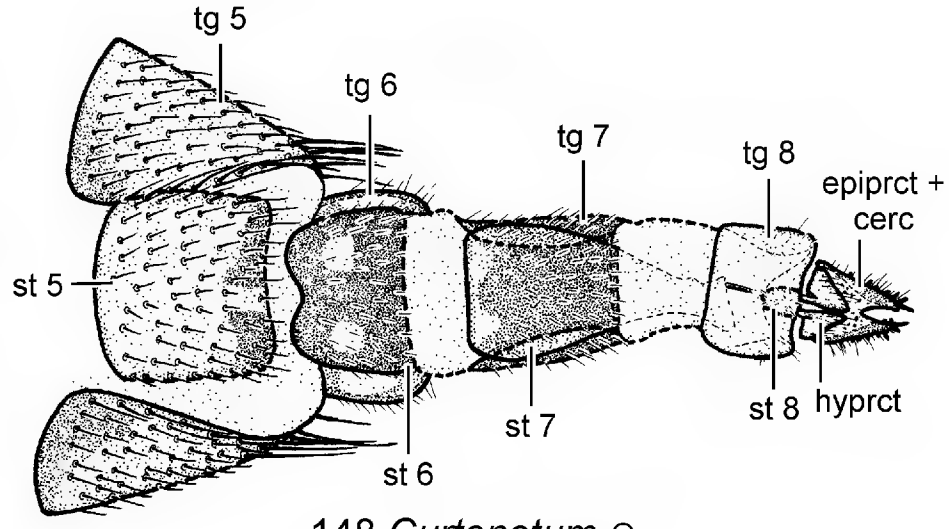
Abbreviations: cerc – cercus; epiprct – epiproct; hyprct – hypoproct; spmth – spermathecae; st – sternite; tg – tergite.

4, 49). The anepisternum has two dark pigmentation patches at the dorsal and ventral anterior margins (Fig. 40) and the male terminalia has the distiphallus apically with a distended and inflated membranous portion (Figs 123, 125). Adults are crepuscular and/or nocturnal and roost during the day in depressions of the forest floor, beneath bushes, shrubs and fallen logs, ditches and the overhangs of stream beds. Some species have been collected at both ground level and from fogged trees in the same areas of South Africa and Uganda (Kirk-Spriggs, in prep.). Some species are larviparous, with multiple ova and first-instar larvae developing in a brood pouch (Figs 136–139), with consequent reduction of the terminal sclerites, giving the abdomen a short, squat appearance (Fig. 135), as opposed to the normal telescopic form of oviparous species (Fig. 146). Females cannot be reliably associated morphologically, so until sexes are associated molecularly, it is unclear which species are larviparous and which oviparous. The larval biology of the genus remains unknown and the immature stages have not been described. The genus requires revision and no identification key to species is currently available.

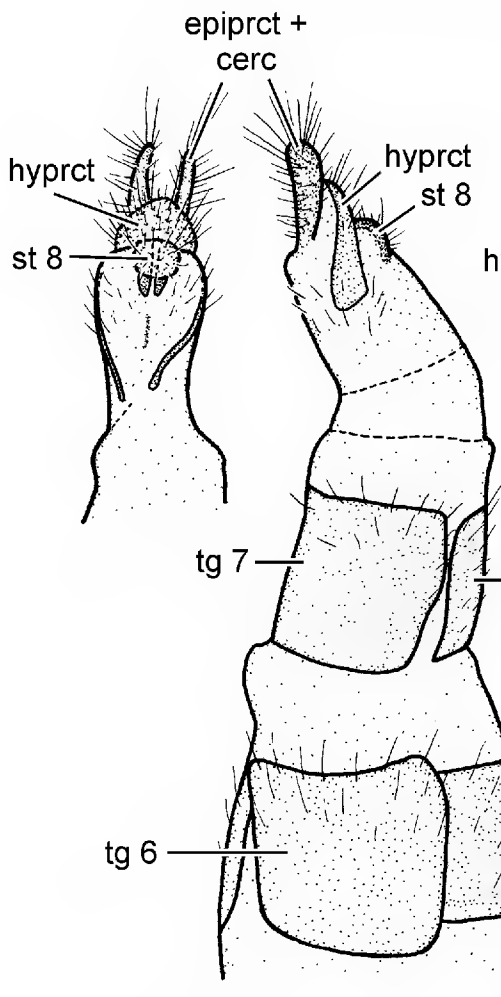
***Cyrtona* Séguy (*sensu lato*).** An endemic genus of three described species (Fig. 1). The two species *Cy. capensis* Hackman, 1960 and *Cy. consobrina* Hackman, 1960, both described from South Africa, belong in a genus of their own and the third species, described as *Parapsinota brevicornis* Duda,



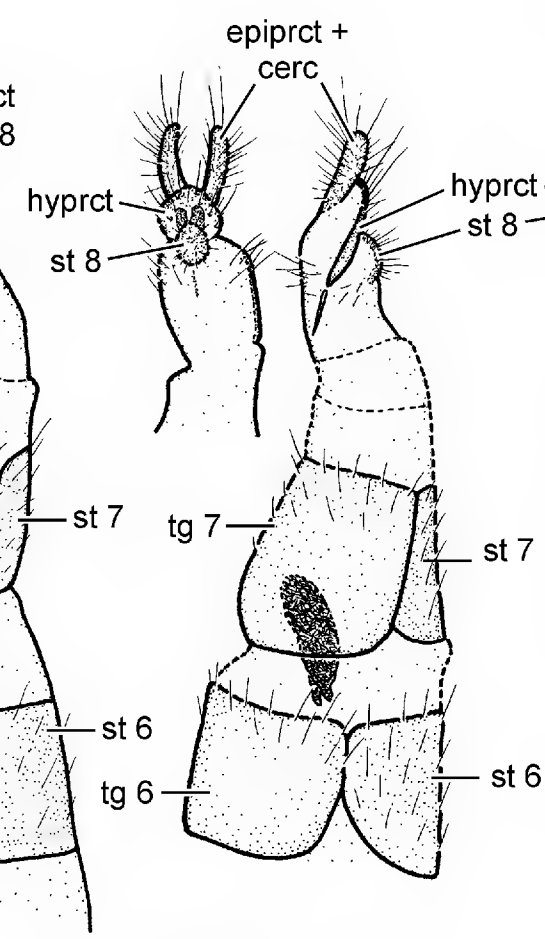
147 *Curtonotum* ♀



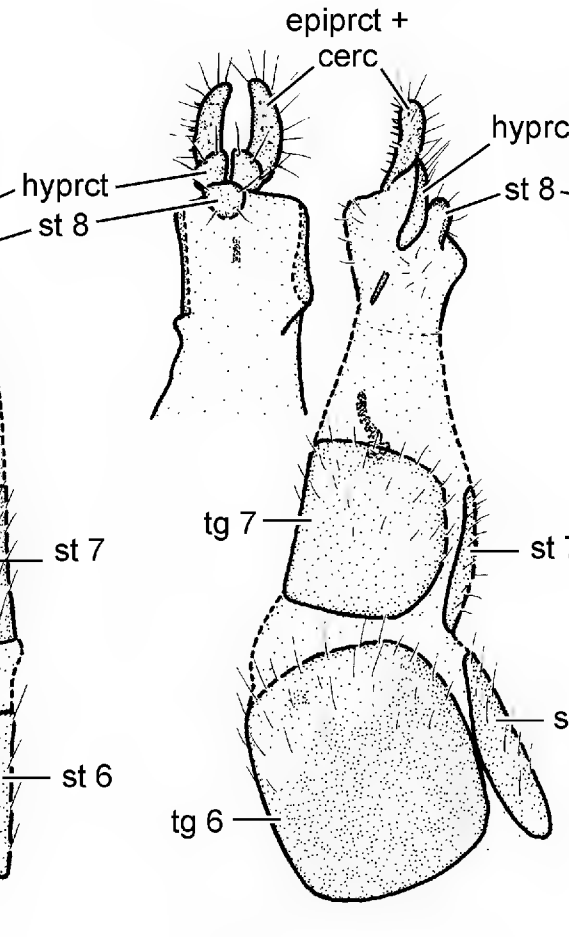
148 *Curtonotum* ♀



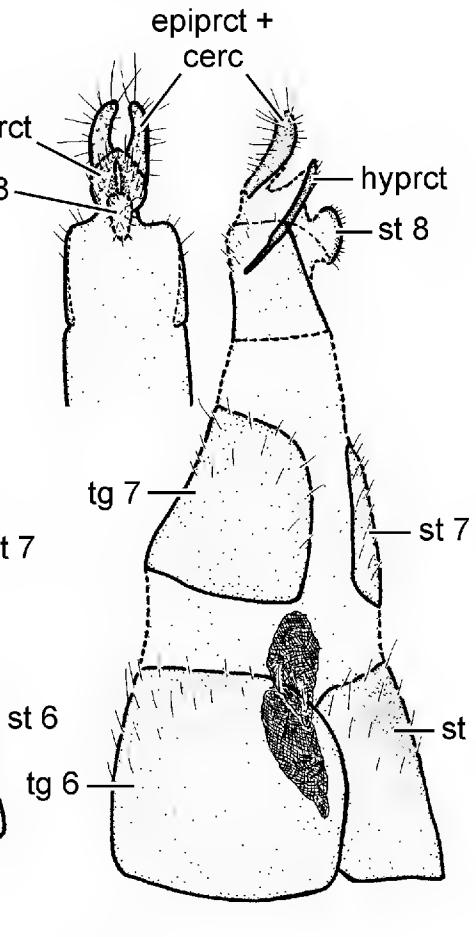
149 *Curtonotum* ♀



150 *Curtonotum* ♀



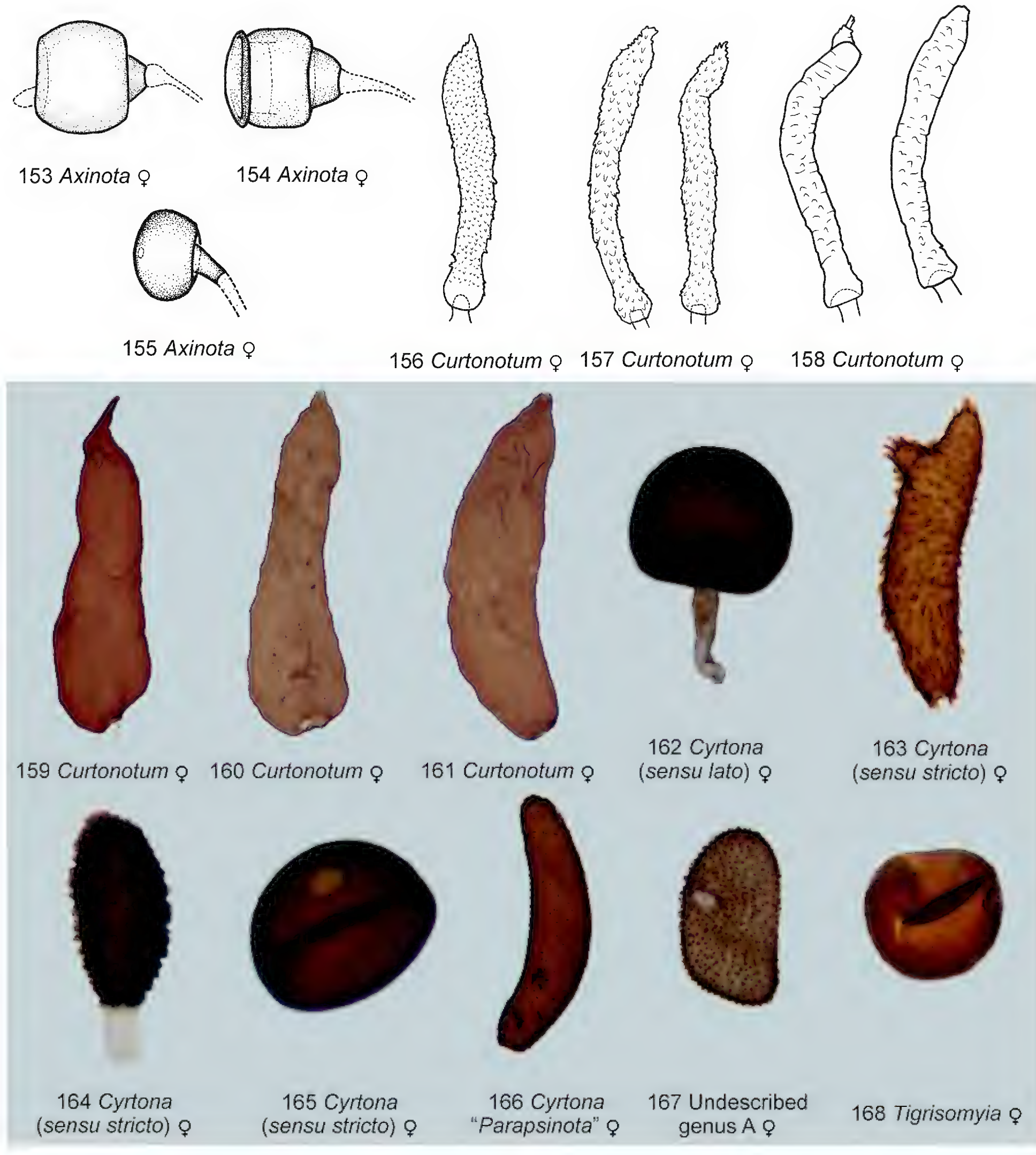
151 *Curtonotum* ♀



152 *Curtonotum* ♀

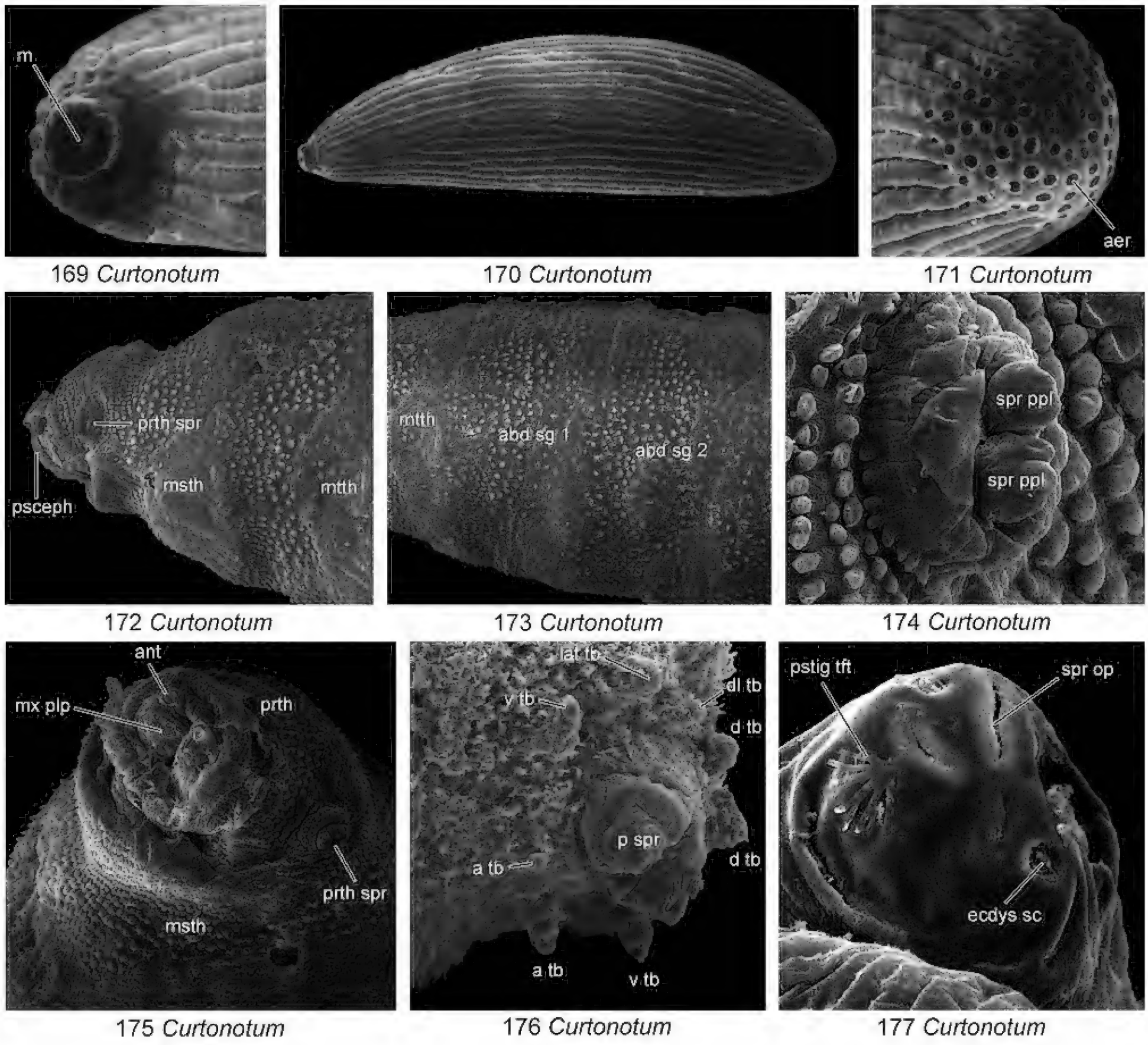
Figs 103.147–152. Female postabdomens of Curtonotidae: (147) *Curtonotum marriott* Kirk-Spriggs, lateral view; (148) same, ventral view; (149) *Cu. campsiphallum* Tsacas, ventral view (left), lateral view (right); (150) *Cu. tsacas* Kirk-Spriggs, ventral view (left), lateral view (right); (151) *Cu. gonzo* Kirk-Spriggs, ventral view (left), lateral view (right); (152) *Cu. simile* Tsacas, ventral view (left), lateral view (right). Figs 147–152 (Kirk-Spriggs & Wiegmann 2013, figs 288, 289, 306–313 © Magnolia Press).

Abbreviations: epiprct + cerc – epiproct + cercus; hyprct – hypoproct; st – sternite; tg – tergite.



Figs 103.153–168. Female spermathecae of Curtonotidae (dorsal views): (153) *Axinota fuscipennis* (Macquart); (154) *A. quasimodoi* Kirk-Spriggs; (155) *A. ahdabi* Kirk-Spriggs; (156) *Curtonotum herrero* Tsacas; (157) *Cu. maculiventris* (Enderlein); (158) *Cu. striatifrons* Malloch; (159) *Cu. marriott* Kirk-Spriggs; (160) *Cu. moffatt* Kirk-Spriggs; (161) *Cu. platyphallum* Tsacas; (162) *Cy.* (*s.l.*) *capensis* Hackman; (163) *Cy.* (*s.s.*) *appendiculata* Séguy; (164) *Cy.* (*s.s.*) *pictipennis* (Thomson); (165) *Cyrtona* (*s.s.*) sp.; (166) *Cy. "Parapsinota"* ? *albomacula* (Curran); (167) Undescribed genus A; (168) *Tigrisomyia amnoni* Kirk-Spriggs. Figs 153–155 (Kirk-Spriggs 2010*a*, figs 25–27), Figs 156–158 (Tsacas 1977, figs 5d, 12f, as *Cu. tigrinum*, 11d), Figs 159–168 (Kirk-Spriggs & Wiegmann 2013, figs 213–215, 82, 84, 83, 81, 86, 85, 80, respectively © Magnolia Press).

1939, also described from South Africa (but omitted by Wirth & Tsacas 1980: 672), is represented by a female holotype only and must be regarded as *insertae sedis*. At least 12 undescribed species are known, which comprise some widespread species and some restricted to higher elevations in the continental Afrotropics or associated with the Cape Fold Mountains and Drakensberg escarpment, extending into the Great Rift Valley. The genus is absent from the Atlantic and Indian oceanic islands, including Madagascar. As here defined, the genus is recognised by the predominantly grey abdomen, or the abdomen



169 *Curtonotum* 170 *Curtonotum* 171 *Curtonotum*

172 *Curtonotum* 173 *Curtonotum* 174 *Curtonotum*

175 *Curtonotum* 176 *Curtonotum* 177 *Curtonotum*

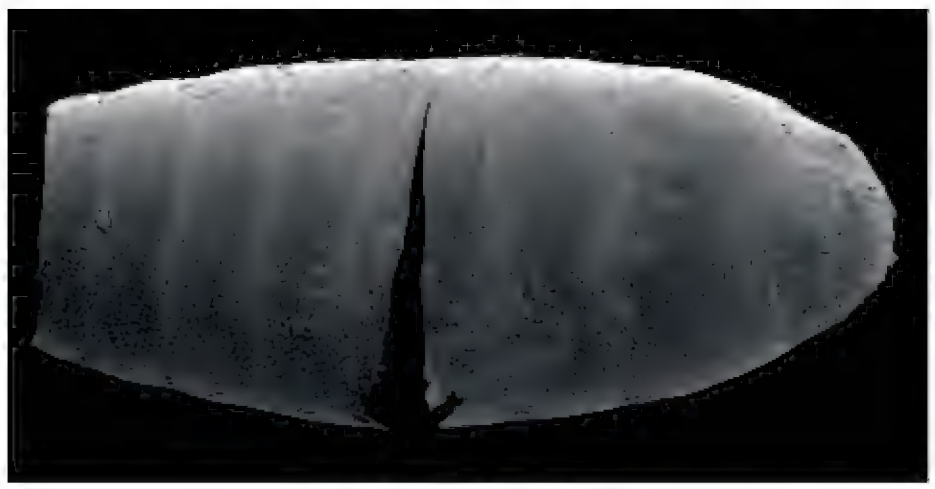
Figs 103.169–177. Immature stages of Curtonotidae: (169) anterior end of egg of *Curtonotum helvum* (Loew), apicolateral view (non-Afrotropical); (170) same, habitus, lateral view; (171) same, posterior end, apicolateral view; (172) anterior end of third-instar larva of *Cu. saheliense* Tsacas (?), lateral view; (173) same, metathorax and abdominal segments 1–2, lateral view; (174) same, prothoracic spiracle, anterolateral view; (175) same, anterior end, ventrolateral view; (176) same, anal division, ventrolateral view; (177) same, posterior spiracle, dorsolateral view. Figs 169–171 (after Meier *et al*. 1997, figs 14, 12, 13, respectively), Figs 172–177 (Kirk-Spriggs 2008*b*, figs 2–4, 6, 10, 12).

Abbreviations: a tb – anal tubercle; abd sg – abdominal segment; aer – aeropyle; ant – antenna; d tb – dorsal tubercle; dl tb – dorsolateral tubercle; ecdys sc – ecdysial scar; lat tb – lateral tubercle; m – micropore; msth – mesothorax; mtth – metathorax; mx plp – maxillary palpus; p spr – posterior spiracle; prth – prothorax; prth spr – prothoracic spiracle; psceph – pseudocephalon; pstig tft – peristigmatic tuft; spr op – spiracular opening; spr ppl – spiracular papilla; v tb – ventral tubercle.

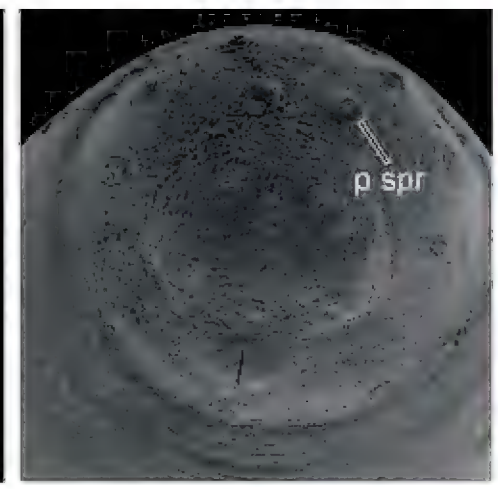
grey with a dark medial facia and/or lateral maculae (Fig. 1). The scutum is not distinctly darkly mottled, but sometimes with pigment patches in the region of the lateral dorsocentral vitta (Figs 1, 47). The anepisternum is unicolourous grey, or has paler yellow pigmentation patches (Figs 1, 38) and the male terminalia have the distiphallus without an apically distended and inflated membranous portion (Figs 113, 115). At this time species can only be delimited on the structure of the male terminalia. Adults are crepuscular and/or nocturnal and are best collected by sweeping just before sunrise or in Malaise traps deployed overnight. Five species were collected by sweeping the base of Table Mountain before daybreak (A.H. Kirk-Spriggs, pers. obs.). The larval biology of the genus remains unknown and the immature stages have not been described, but all species examined appear to be oviparous. The genus requires revision and no identification key to species is currently available.

Undescribed genus A. An undescribed endemic genus of several undescribed species mostly distributed in Central Africa. The genus is absent from the Atlantic and Indian oceanic islands, including Madagascar. As here defined, the genus is recognised by the wing membrane with a diffuse darker marking in the anterior $^1/_2$ (in cells r_1, r_{2+3}, r_{4+5}), at the base of cell r_1, over the *dm–m* crossvein and along vein M_4 dorsally in cell m_1 (Fig. 82). The scutum has a uniform pale brown ground colour and paler brown dorsocentral vittae (Fig. 50). The subscutellum is wide and bulging (Fig. 63). The male terminalia are greatly reduced (Figs 126, 127), the phallapodeme is triangular, the phallic plate is ventrally tapering, with the basiphallus subequal to the sclerotised part of the distiphallus (Fig. 127). At this time species can only be delimited on the structure of the male terminalia. Specimen labels indicate that most species are associated with lowland tropical forest habitats. The larval biology and immature stages remain unknown.

Undescribed genus B. An undescribed endemic genus with at least one undescribed species from West Africa (Nigeria). As here defined, the genus is recognised by the setose disk of the scutellum (Fig. 51). The scutum has the ground colour uniformly dark chestnut brown, without dorsocentral vittae (Fig. 51). The wing membrane is diffusely darkened in the apical $^1/_2$ and over the *r–m* and *dm–m* crossveins (Fig. 83) and the alula is squarely (not evenly) rounded (Fig. 83). The scutellum is concolourous with the scutum (Fig. 51) and the male terminalia has the surstylus subdivided (Fig. 128). At this time species can only be delimited on the structure of the male terminalia.

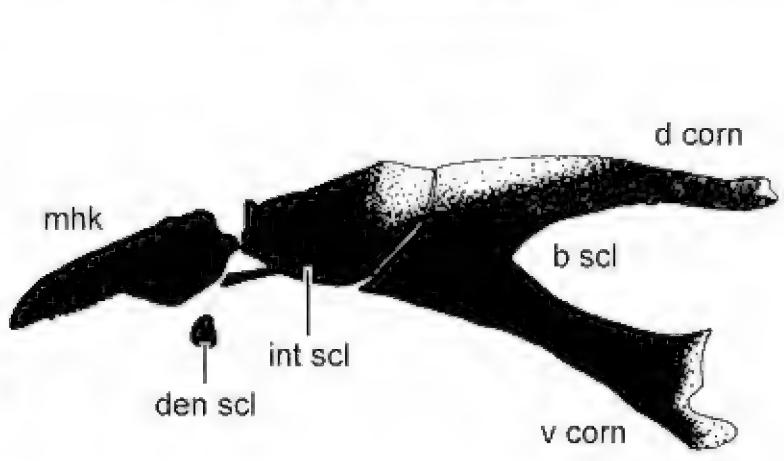


178 *Curtonotum*

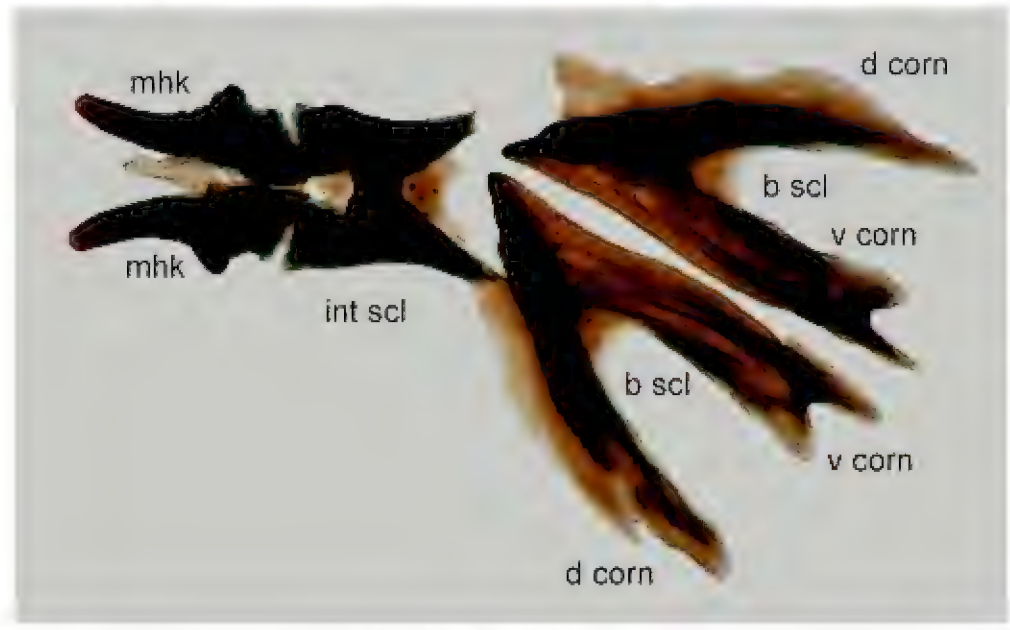


179 *Curtonotum*

180 *Curtonotum*



181 *Curtonotum*



182 *Curtonotum*

Figs 103.178–182. Immature stages of Curtonotidae: (178) puparial trunk of *Curtonotum simile* Tsacas, lateral view; (179) same, posterior end of puparium, posteroventral view; (180) same, *Cu. saheliense* Tsacas; (181) cephaloskeleton of *Cu. simile*, lateral view; (182) same, dorsal view. Figs 178–180, 182 (Kirk-Spriggs 2008*b*, figs 13, 25, 18, respectively), Fig. 181 (Greathead 1958, fig. 1, as *Cyrtonotum cuthbertsoni*).

Abbreviations: b scl – basal sclerite; d corn – dorsal cornu; den scl – dental sclerite; int scl – intermediate sclerite; mhk – mouthhook; p spr – posterior spiracle; v corn – ventral cornu.

Nothing is known of the biology of the genus and the immature stages remain unknown.

Undescribed genus C. An undescribed endemic genus with at least three undescribed species restricted to the Drakensberg escarpment of South Africa. As here defined, the genus is recognised by the wing membrane, which is uniformly brownish and unmarked, with the anal lobe distinctly broadened, but without an auxiliary vein on vein M_1 (Fig. 84). The scutal setae do not have dark marks around the bases of the sockets (Fig. 52). The central dorsocentral vittae do not extend onto scutellum (Fig. 52). The antennal arista is short-pubescent (Fig. 24). The male terminalia have the surstylus grossly enlarged and semicircular, which is clearly visible in undissected males (Fig. 130), the phallus is greatly reduced in size and foreshortened, with the phallapodeme sub-triangular and the basiphallus length is sub-equal to the length of the phallapodeme (Fig. 131). At this time species can only be delimited on the structure of the male terminalia. Specimen labels indicate that the genus probably occurs in upland grassland habitats and may be associated with *Protea* (Proteaceae) flowers. The biology and immature stages otherwise remain unknown.

***Tigrisomyia* Kirk-Spriggs.** An endemic genus of four species (Fig. 5), confined to the Usambara (Eastern Arc) Mountains and Malawi Rift Valley forests of East Africa: the more widespread *T. amnoni* Kirk-Spriggs, 2010, described from Malawi, Tanzania and Zambia; *T. kinskii* Kirk-Spriggs, 2010, from Malawi; *T. rhayaderi* Kirk-Spriggs, 2010, from Kenya and Malawi; and *T. scoliosis* Kirk-Spriggs, 2010, from Tanzania. No additional undescribed species are known. The genus is easily distinguished from other genera of curtonotids by the frons black to brown, extensively yellow in the anterior half, with the surface pitted, but shiny (Figs 17, 25). The scutum is strikingly marked with a silver-dusted triangular macula anterior to the transverse suture laterally (Figs 69–71) and a dark macula posterior to the transverse suture and a dark fascia at the anterior margin (Figs 69–71). The scutum has the disk either uniform black to grey, or predominately brown with longitudinal paler dorsocentral vittae (Figs 69, 70). The wing is relatively narrow, with the membrane faintly infuscate yellow throughout (Fig. 85) The abdomen is black and yellow banded (Figs 5, 53) and the male terminalia are highly derived (Figs 132, 133). The genus has been collected in montane rainforest and Miombo woodlands and has been sampled in Malaise traps over permanent and ephemeral water courses in Malawi (A.H. Kirk-Spriggs, pers. obs.). The immature stages remain unknown. Kirk-Spriggs (2010*b*) provided an identification key, mapped the distribution of the four species (fig. 24) and discussed biogeographical implications.

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DIASTATIDAE 104

(incl. Campichoetidae) (Diastatid Flies)

Ashley H. Kirk-Spriggs and Wayne N. Mathis

Fig. 104.1. Female of *Diastata freidbergi* Barraclough (non-Afrotropical) (photographs © S.A. Marshall).

Diagnosis

Small (body length: 2.5–4.0 mm), greyish brown to black shiny drosophilid-like acalyptrate flies; often with patterned wings and weakly spinose costal vein (Fig. 1).

Head (Figs 6, 7) with postocellar setae convergent; both inner and outer vertical setae present; ocellar and vibrissal setae well-developed; 2 well-developed fronto-orbital setae, proclinate seta laterad of reclinate seta; antenna decumbent; arista elongate, macro-pubescent (Fig. 7) or short plumose (Fig. 6).

Thorax with anepisternum setulose (*Diastata* Meigen) or seta absent (*Campichoeta* Macquart and *Euthychaeta* Loew); katepisternum bearing 1–2 setae, if 2 then posterior seta longer. Wing (Figs 2–5) with costal vein (*C*) extended to vein M_1 (Fig. 2); costal vein broken once (subcostal break only in *Campichoeta* (Fig. 5) and *Euthychaeta*), or twice (humeral and subcostal breaks in *Diastata* (Fig. 2)); subcostal vein (*Sc*) incomplete, not reaching costal vein, often fused with vein R_1 distally (Fig. 2); vein R_1 bare; both veins *CuA*+*CuP* and A_1 present (Fig. 5); cell *cua* closed, crossvein *bm–m* present (Fig. 2); Afrotropical *Diastata* with wing infuscate in region of cell r_1 (basally or

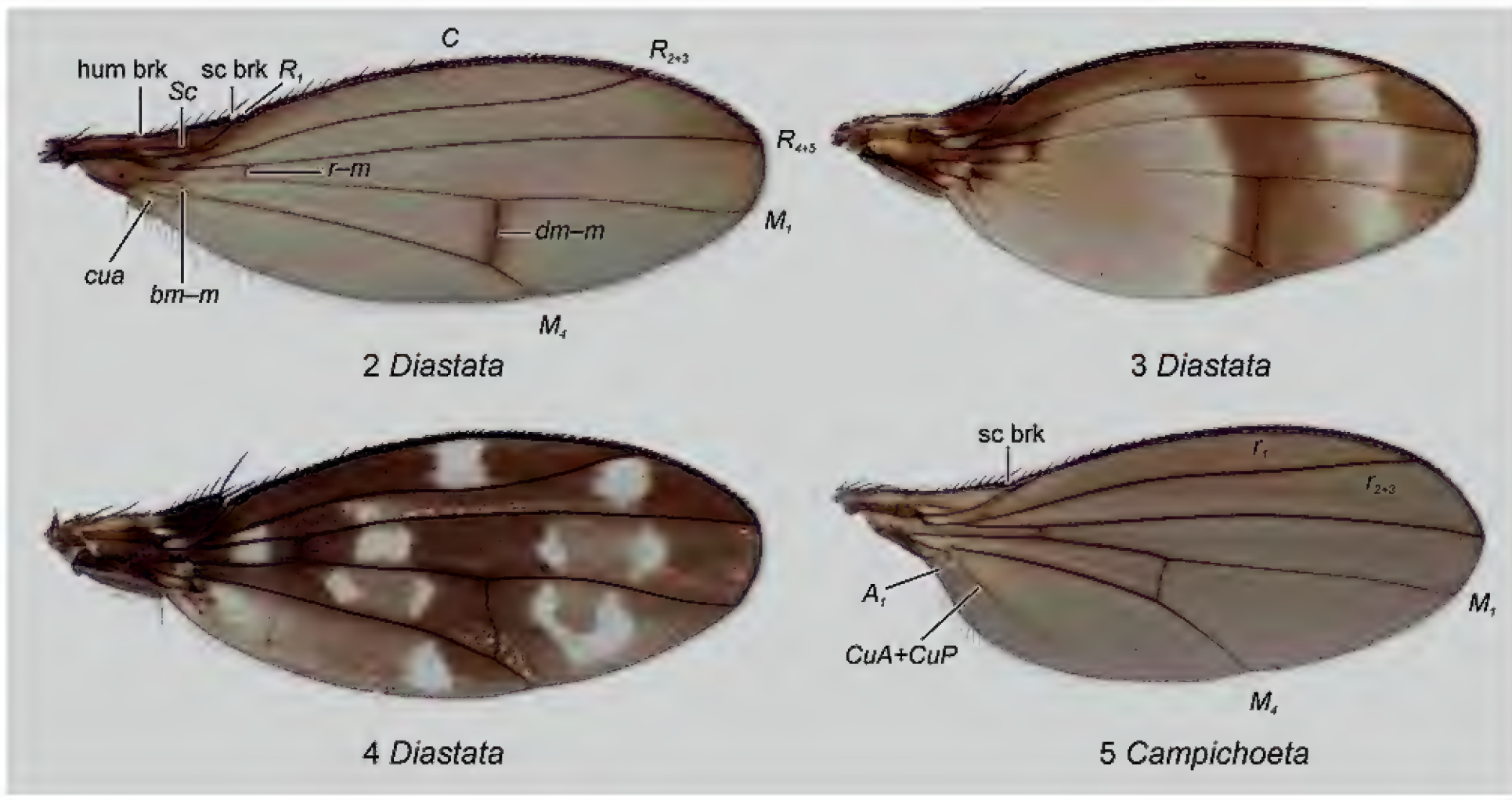
Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2021. Manual of Afrotropical Diptera. Volume 3. Brachycera—Cyclorrhapha, excluding Calyptratae. *Suricata* 8. South African National Biodiversity Institute, Pretoria; pp. 2283–2288.

more extensively) and over crossvein *dm–m* (Fig. 2), banded (Fig. 3) or maculate (Fig. 4); Afrotropical *Campichoeta* with wing membrane uniformly faintly infuscate to hyaline (Fig. 5), slightly infuscate in region of cells r_1 and r_{2+3} (Fig. 5). Legs moderately elongate, slender (Fig. 1).

Abdomen (Fig. 8) with segments 1–5 unmodified; male with segments 6–8 reduced, although syntergite 7 + 8 well-developed, sternite 7 lacking; abdominal spiracles (6 or 7) in membrane; male terminalia (Figs 9–11) with epandrium relatively broad in lateral view; surstylus usually unilobate (*Campichoeta* and *Euthychaeta*) or bilobate (*Diastata*) (Figs 9, 10), solidly fused with epandrium or freely articulated, occasionally absent; cercus short, rather fleshy; hypandrium heavily sclerotised, U-shaped; hypandrium heavily sclerotised, U-shaped, distally blade-like; pregonite and postgonite closely applied to base of phallus; phallus rigidly sclerotised, frequently C-shaped in lateral view; phallapodeme rod-like with expanded apex, free from hypandrium; female (Fig. 8) with ventral receptacle well-sclerotised (*Diastata*) (Fig. 8, inset) or membranous (*Campichoeta* and *Euthychaeta*); female postabdomen with cerci free from each other, with numerous setulae (Fig. 8); 2 spermathecae present, sclerotised (*Campichoeta* and *Euthychaeta*) or unsclerotised (*Diastata*).

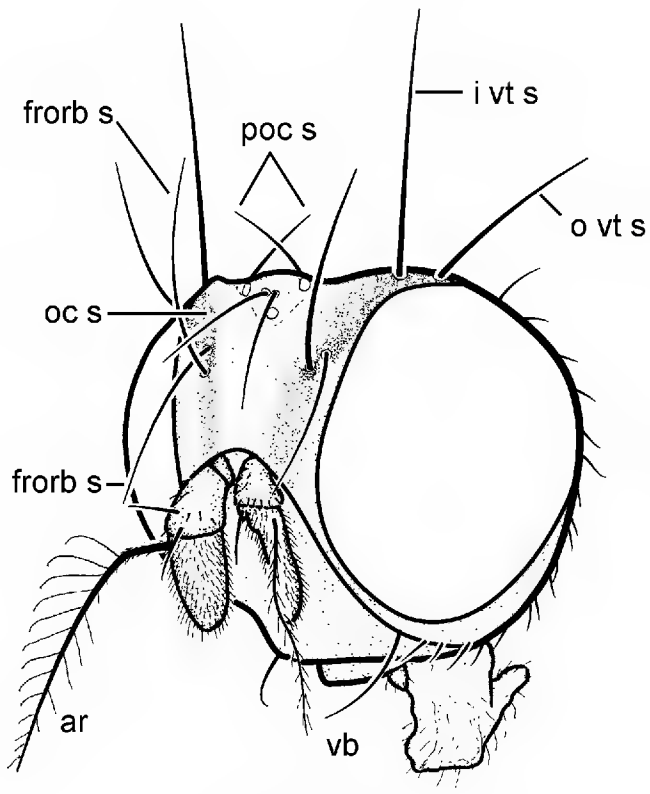
Puparium (based on description provided by Rotheray (2008) for non-Afrotropical *D. costata* Meigen, 1830; the egg and larval stages of Diastatidae remain unknown): length 2.5 mm, width 1.2 mm; truncate anteriorly and posteriorly (Fig. 12); integument matt without vestiture; dorsum of abdominal segments 1–7 with creeping welts loosely arranged in 4 bands; ventral creeping welts formed of numerous inclined rows, occupying *ca* ½ segment; all spicules of equal size; prothoracic spiracles divided medially, with posterior arm broader than anterior, with 4–5 spiracular papilla on each arm; caudal end of last abdominal segment (Fig. 13) with 6 pairs of triangular, sub-equally sized fleshy projections surrounding posterior spiracles; posterior spiracles inserted on elongate, fleshy protuberances, with 3 spiracular openings on each spiracle arranged radially around ecdysial scar; cephaloskeleton (Fig. 14) strongly sclerotised; mouthhooks separate, with sub-rectangular base and broad, slightly curved anterior hook; comma-shaped dental sclerite present beneath mouthhooks; intermediate sclerite narrow in lateral view and expanded in dorsal view, posteriorly separated from basal sclerite; basal sclerite with dorsal and ventral cornu of approximately same length, dorsal cornu with unpigmented horizontal strip in apical ½; ventral cornu without cibarial ridges in cibarium; parastomal bar extends over intermediate sclerite and dorsal bridge present.

Adult Diastatidae are superficially similar to Drosophilidae (see Chapter 108), especially the genus *Clastopteromyia* Malloch, and to Opomyzidae (see Chapter 84), but are

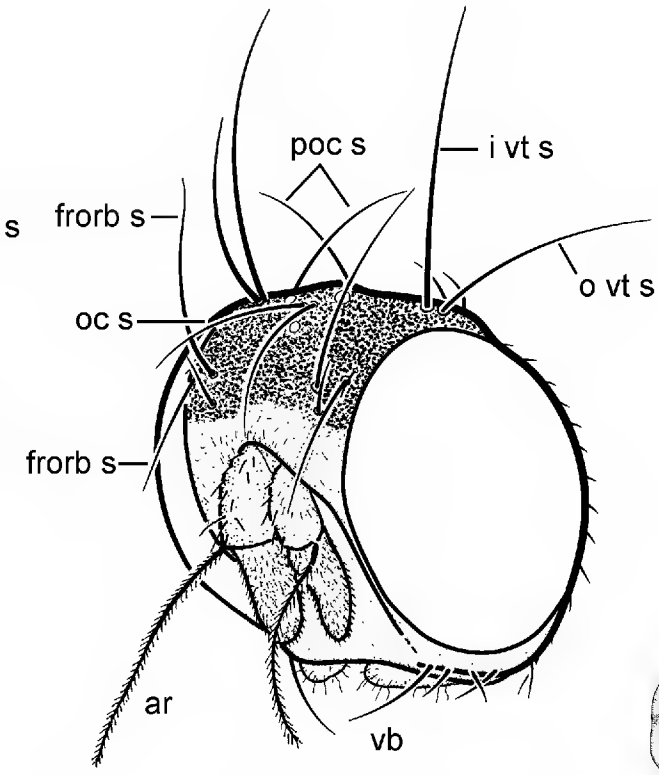


Figs 104.2–5. Wings of Diastatidae *sensu lato* (dorsal views): (2) *Diastata montana* Cogan; (3) *D. tsacasi* Cogan; (4) *D. carolinae* Cogan; (5) *Campichoeta natalensis* Barraclough.

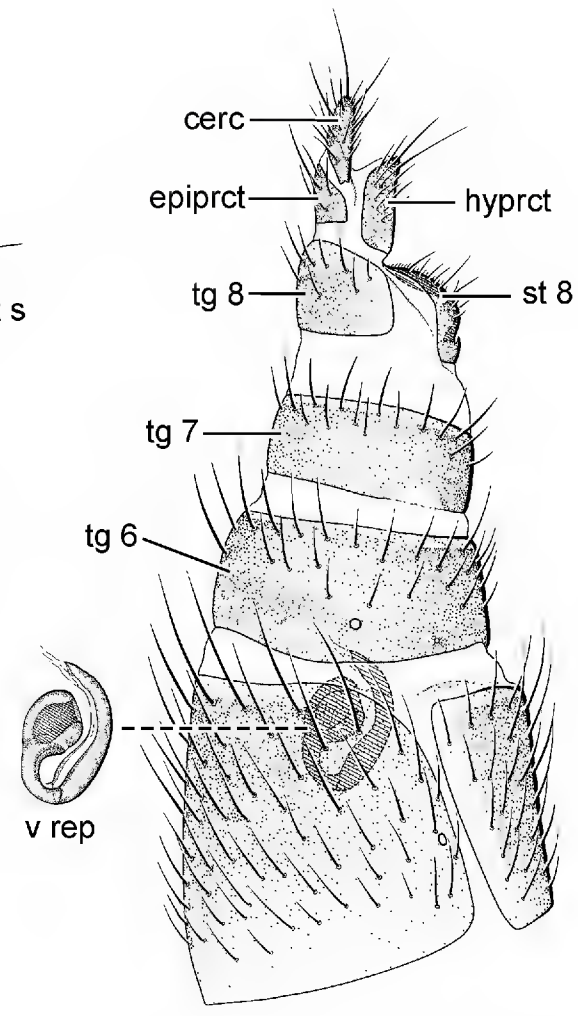
Abbreviations: A_1 – first branch of anal vein; *bm–m* – basal medial crossvein; *C* – costal vein; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *cua* – anterior cubital cell; *dm–m* – discal medial crossvein; hum brk – humeral break; M_1 – first branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; r_1 – first radial cell; R_{2+3} – second branch of radius; r_{2+3} – second + third radial cells; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Sc* – subcostal vein; sc brk – subcostal break.



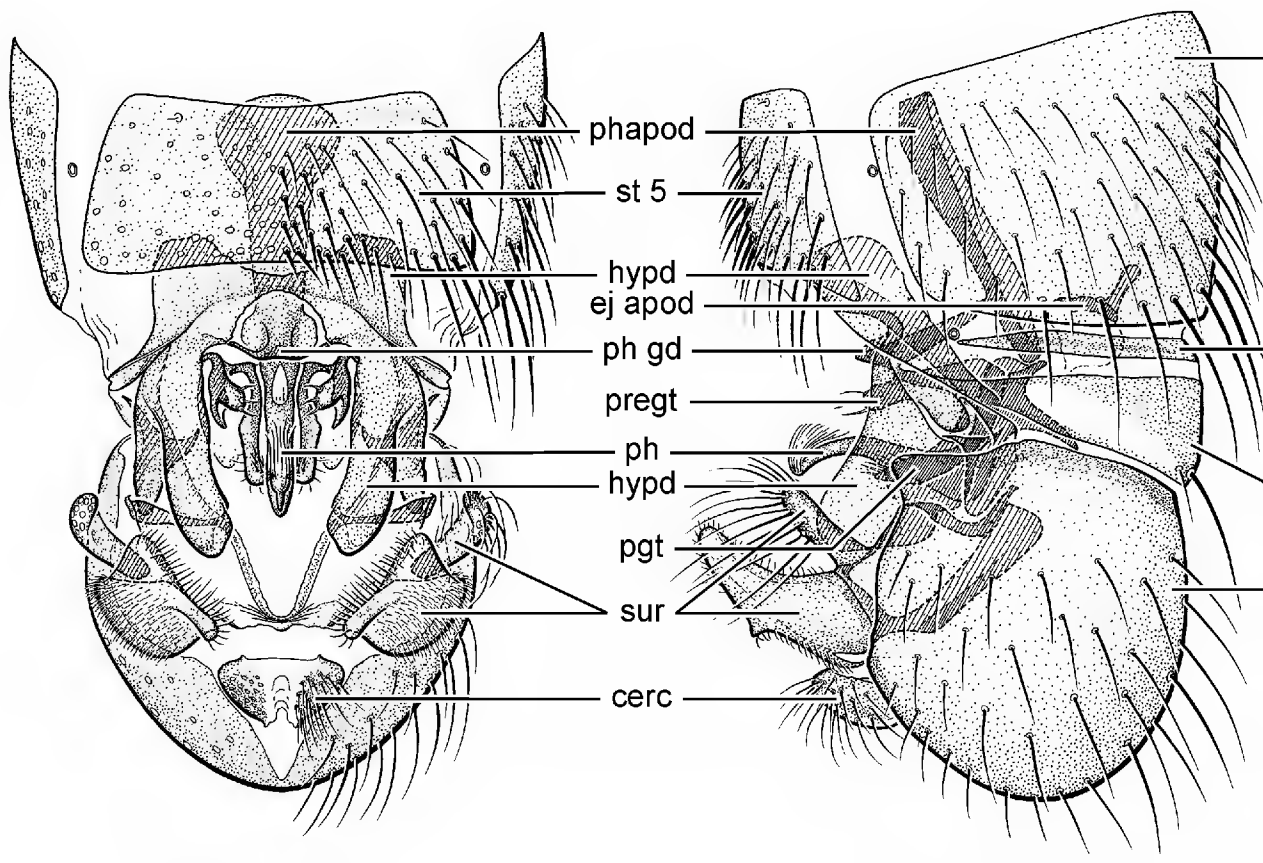
6 *Diastata* ♂



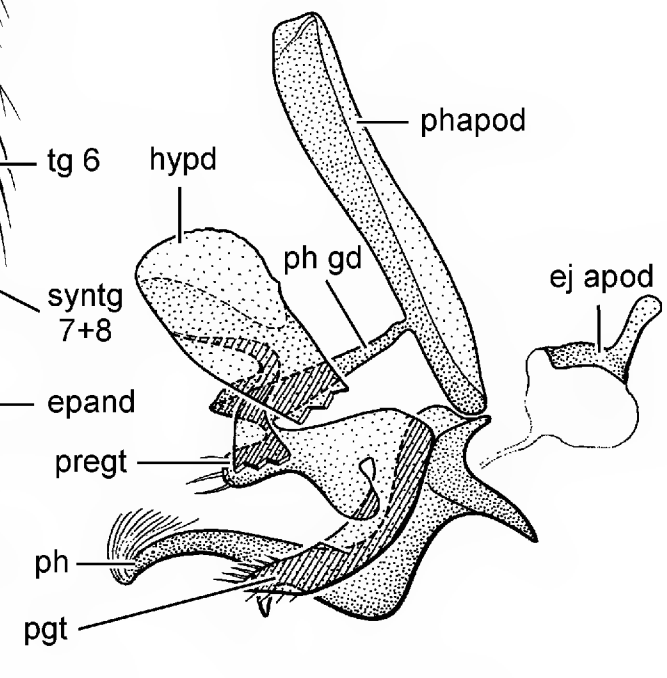
7 *Campichoeta* ♂



8 *Diastata* ♀



9 *Diastata* ♂



10 *Diastata* ♂

11 *Diastata* ♂

Figs 104.6–11. Heads, female abdomen and male terminalia of Diastatidae *sensu lato*: (6) head of *Diastata montana* Cogan, dorsolateral view ♂; (7) same, *Campichoeta natalensis* Barraclough ♂; (8) female abdomen of *D. vagans* Loew, lateral view (non-Afrotropical); (9) same, male terminalia, ventral view; (10) same, lateral view; (11) same, phallic complex, lateral view. Figs 8–11 (McAlpine 1987, figs 4, 8, 9, 7, respectively).

Abbreviations: ar – arista; cerc – cercus; ej apod – ejaculatory apodeme; epand – epandrium; epiprct – epiproct; frorb s – fronto-orbital seta; hypd – hypandrium; hyprct – hypoproct; i vt s – inner vertical seta; o vt s – outer vertical seta; oc s – ocellar seta; pgt – postgonite; ph – phallus; ph gd – phallic guide; phapod – phallapodeme; poc s – postocellar seta; pregt – pregonite; st – sternite; sur – surstylus; syntg – syntergite; tg – tergite; v rep – ventral receptacle; vb – vibrissa.

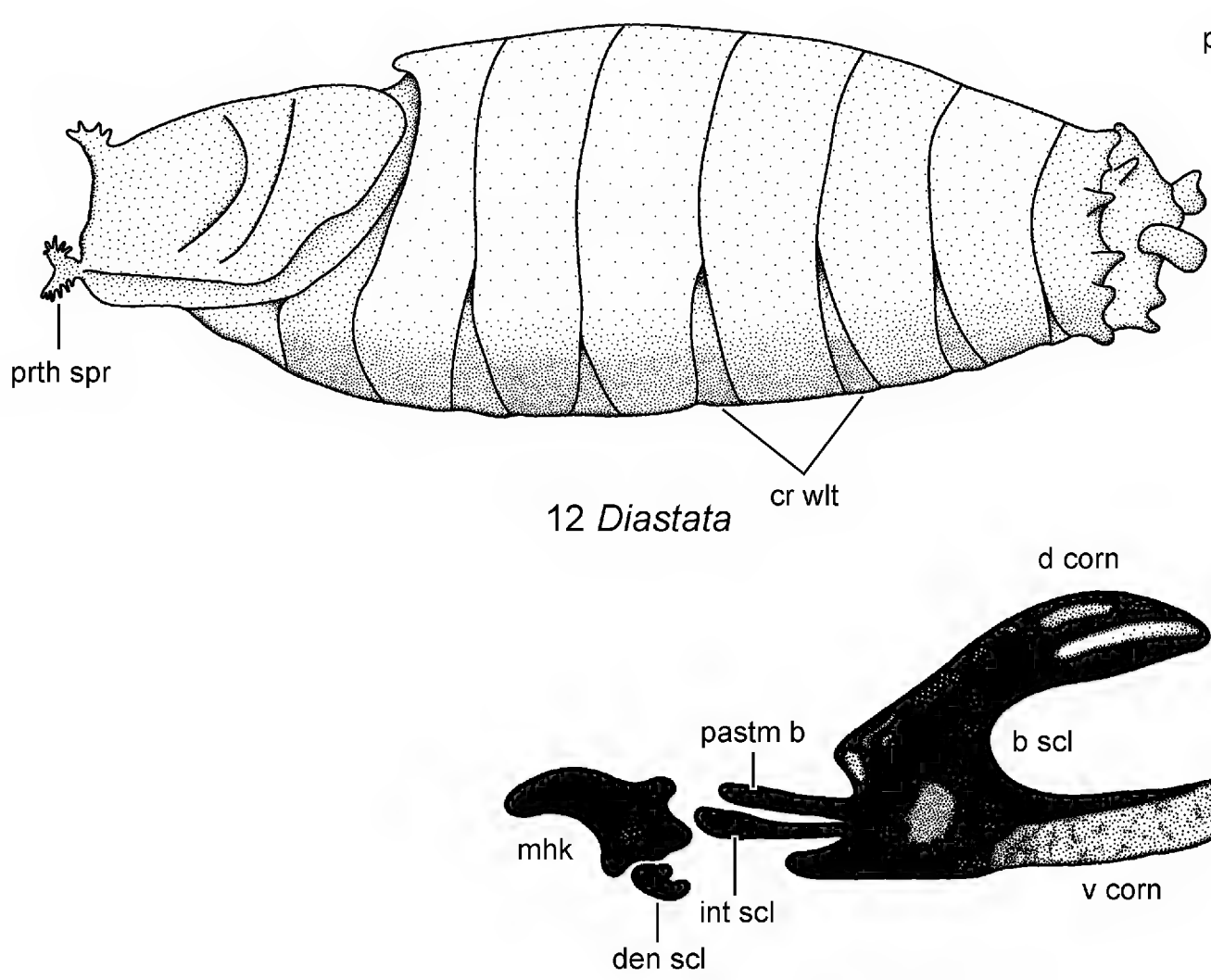
distinguished from either of these two families in having 2 large fronto-orbital setae (1 in Opomyzidae), by the dorsolateral position of the large proclinate fronto-orbital seta relative to the reclinate fronto-orbital seta and often by the weakly spinose costal margin. Drosophilidae also have 2 costal breaks, but a bare anepisternum. Opomyzidae have a seta on the anepisternum, but like *Campichoeta*, they lack the humeral costagial break. Opomyzidae are distinguished by the subcostal break being well-separated from vein R_1, while it is close to R_1 in Diastatidae (*sensu lato*) and Drosophilidae. In addition, *Diastata* has a setulose anepisternum and 2 costal breaks and in *Campichoeta* the anepisternum is bare and only has 1 costagial break. Diastatidae may also be superficially confused with some Curtonotidae (see Chapter 103), but are easily distinguished by the presence of crossvein *bm–m* (cells *bm* and *dm* confluent, *i*.e., crossvein *bm–m absent* in Curtonotidae), and the position of the fronto-orbital setae.

Biology and immature stages

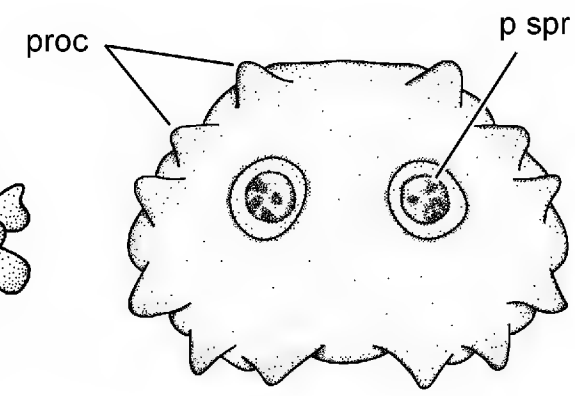
Diastatidae are a small family that occurs primarily in temperate zones, where there is greater diversity. The few species that are known from tropical regions, including Afrotropical species, have almost exclusively been collected at higher elevations. There is greater species diversity in the Palaearctic Region, which is probably reflective of the true species richness, but also that this fauna is better known and more recent research is available. The northern temperate fauna includes several species that are widespread and have Holarctic distributions, although both the Palaearctic and Nearctic Regions also have endemics. The family is noticeably absent from the Australasian Region and the Oriental Region is represented by a single species (Mathis & Barraclough 2011).

Little is known regarding the immature stages of Diastatidae. The puparium of the Palaearctic species, *D. costata* was described by Rotheray (2008) (see above), who figured the pupal habitus, prothoracic spiracles and the caudal end of the puparium. The third-instar larva of *Campichoeta* was described by Hennig (1952) (as *Thryptochaeta tristis* Fallén, 1823 = *Campichoeta basalis* (Meigen, 1830)).

Adults of *Diastata* usually occur on low deciduous shrubs along the margins of marshes, bogs, damp woodlands and other lush habitats. *Campichoeta* likewise frequents lush, low vegetation, especially where such habitats occur in otherwise dry to arid environments, such as found in the American southwest, or in Mediterranean countries (Ferrar 1987: 139; Hennig 1952).



12 *Diastata*



13 *Diastata*

14 *Diastata*

Figs 104.12–14. Immature stages of Diastatidae *sensu lato*: (12) habitus of puparium of *Diastata costata* Meigen, dorsolateral view (with partially detached dorsal puparial cap) (non-Afrotropical); (13) same, caudal view; (14) same, pupal cephaloskeleton, lateral view. Figs 12–14 (after Rotheray 2008, figs 1, 4, 2, respectively).

Abbreviations: b scl – basal sclerite; cr wlt – creeping welts; d corn – dorsal cornu; den scl – dental sclerite; int scl – intermediate sclerite; mhk – mouthhook; p spr – posterior spiracle; pastm b – parastomal bar; proc – processes; prth spr – prothoracic spiracle; v corn – ventral cornu.

Economic significance

The family Diastatidae (*sensu lato*) is not known to have any economic significance and no cases of agricultural, medical or forensic significance are noted in the literature.

Classification

The phylogenetic relationships among taxa here included in the Diastatidae remain unresolved, although varying classifications have been proposed (Chandler 1998*a*: 519, 1998*b*: 525). *Diastata* is sometimes treated alone (Chandler 1987, 1998*b*), as an included lineage within the Ephydridae (Griffiths 1972: 111), with *Campichoeta*, *Euthychaeta* and the fossil genus *Pareuthychaeta* Hennig grouped in the separate family Campichoetidae (Chandler 1987, 1998*a*: 515, 1998*b*: 523; Griffiths 1972). An alternative is to recognise all four genera in a single family (Barraclough 1992; McAlpine 1987: 1019, 1989: 1490), although it is probably paraphyletic, with respect to Camillidae and Ephydridae. The classification adopted here is deliberately conservative, with *Campichoeta* and *Diastata* alone in the family, awaiting more definitive resolution. Grimaldi's (1990: 8–12) cladogram of the Ephydroidea placed the family Camillidae as the sister-group to the Ephydridae (non-Afrotropical Risidae are included in the Ephydridae) and then with the Diastatidae as the sister-group to the combined clade of Camillidae + Ephydridae. This cladogram recognised Campichoetidae as a separate family and as a sister-group to Diastatidae + Camillidae + Risidae + Ephydridae, so Diastatidae in the context of Grimaldi's cladogram was the genus *Diastata* only. In a more recent molecular phylogeny, Wiegmann *et al*. (2011) place the Camillidae as the sister-group to the Curtonotidae + Diastatidae. Conclusions from this last paper regarding acalyptrate relationships should, however, be treated with caution.

Identification

The paper and book chapters by Chandler (1987, 1998*a*, 1998*b*) are essential for an understanding of the Diastatidae (*sensu lato*) and also include identification keys to genera. Most identification keys to the family are problematic, as they do not recognise that the costa of *Diastata* is broken twice (humeral and subcostal breaks) (e.g., Fig. 2), whereas that of *Campichoeta* is broken just once (subcostal break) (e.g., Fig. 5). Moreover, McAlpine's identification key (1987) to genera is faulty in that the anepisternum, not the katepisternum (as referred to), is either setulose, or bare. Afrotropical Diastatidae were catalogued by Cogan (1980*a*), although this work is now outdated. The most important papers for the identification of Afrotropical species are Cogan (1975, 1980*b*) and Barraclough (1992, 1994). Adults are usually hand-collected or are sampled using Malaise traps deployed in suitable habitats. Adults are best preserved dry and should be micro-pinned in the field for later double-mounting (see Chapter 2).

Key to genera of Afrotropical Diastatidae (*sensu lato*)

1. Antennal arista plumose, with longer branches dorsally (Fig. 6); head with large reclinate fronto-orbital seta, lacking shorter reclinate fronto-orbital seta anterior to it (Fig. 6); thorax with anepisternum setulose; wing infuscate in region of cell r_1 (basally or more extensively) and over crossvein *dm–m* (Fig. 2), banded (Fig. 3) or maculate (Fig. 4), with costal vein (C) with both humeral and subcostal breaks (Fig. 2). . . . . *Diastata* Meigen

– Antennal arista with short pubescence only (Fig. 7); head with large reclinate fronto-orbital seta inserted behind shorter reclinate fronto-orbital seta (Fig. 7); thorax with anepisternum bare; wing faintly infuscate to hyaline, with costal vein (C) with subcostal break only (Fig. 5). . . . . *Campichoeta* Macquart

Synopsis of the fauna

The family Diastatidae (*sensu lato*) is divided into three extant genera: *Euthychaeta* (Palaearctic, monotypic), *Campichoeta* and *Diastata*; the last two named occur in the Afrotropical Region. The group was most recently reviewed by Mathis (2010) and Mathis & Barraclough (2011).

***Campichoeta* Macquart.** A genus of 12 valid species occurring in the Afrotropical, Nearctic, Oriental and Palaearctic Regions. Two species occur in the Afrotropics: *C. edwardsi* Barraclough, 1992, from Ethiopia and Kenya in Afromontane forest at elevations of 1,500–3,000 m and *C. natalensis* Barraclough, 1992, from eastern South Africa, both of which were described and keyed by Barraclough (1992) and were until recently only known from the type series. The two species are distinguishable on the colour of the face, propleural region and sternite 1. Barraclough (1992) suggested that habitats are likely to be similar to those of Holarctic species, such as rich herbaceous vegetation in, and adjacent to, moist woodland, often along stream banks. There is recent material of *C. natalensis* (including the unknown male), in the National Museum, Bloemfontein, sampled in the eastern Free State Province, South Africa, in *Leucosedea*-dominated scrub, at an elevation of 1,660 m (42.5 km from the edge of the true Drakensberg escarpment and 31.3 km from the type locality) and one female specimen sampled in the Western Cape Province, South Africa, from *Acacia* valley woodland, at an elevation of only 336 m (870 km from the type locality). All the aforementioned material was sampled in Malaise traps deployed over slow-flowing, vegetated streams. These records indicate that the genus is more widely distributed than previously thought and is not confined to medium- to high-elevation Afromontane forest.

***Diastata* Meigen.** A genus of 35 valid species occurring in all zoogeographical regions, except Australasia and Antarctica. Ten species occur in the Afrotropical Region of which eight were keyed by Barraclough (1992). Later, Barraclough (1994) described two additional species, *D. afrocuta*, from Kenya and *D. freidbergi* from Tanzania, and provided a key to the two East

African species. Species of the genus are distinguished externally on subtle distinctions in wing pattern and characters of the thoracic pleura, mesonotum and frons. Most species can only be reliably identified by reference to the male terminalia. Barraclough (1992) discussed the biogeography of the Afrotropical species and noted they exhibit a typical boreal distribution, being virtually restricted to montane regions in tropical areas, but also at lower elevations in temperate parts of South Africa. Specimens are rarely collected and additional undescribed species are expected in suitable montane habitats.

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BRAULIDAE 105

(Bee Louse Flies)

Burgert S. Muller

Fig. 105.1. *Braula coeca* Nitzsch on honeybees (non-Afrotropical) (photograph © P. Kozak).

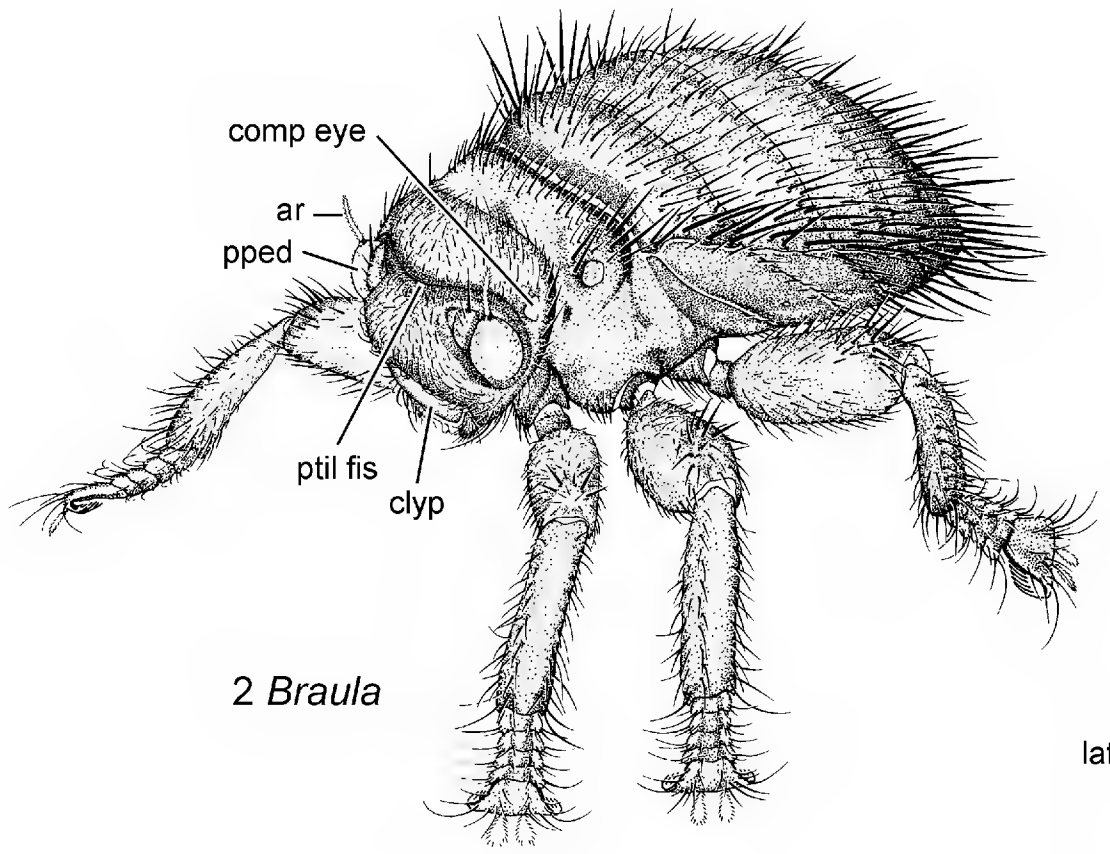
Diagnosis

Small-sized (body length: *ca* 1–2 mm), compact, apterous acalyptrate flies (Figs 1, 2), generally reddish brown in colour, sclerotised, with head shortened, compound eyes reduced and ocelli absent (Fig. 2); body uniformly clothed in stiff, bristle-like setae (head and legs also with setulae), typically setae longer on lateral margins of all segments and posteriorly on apical abdominal segments, head and tarsi (Fig. 2); legs with tarsal claws modified and comb-like (Fig. 3); phoretic, commensalistic association with honeybees, *Apis* species (Apidae), with immature stages occurring in wax combs; adults typically attached to queens and workers, occasionally drones.

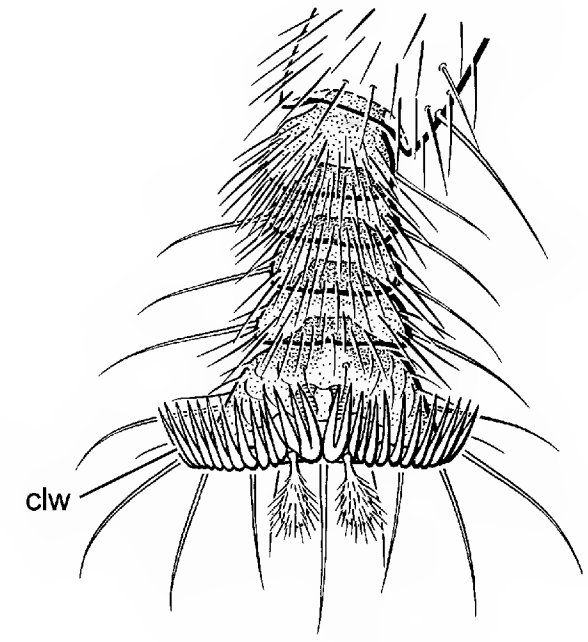
Head (Fig. 2) compressed anteroposteriorly, somewhat wider than thorax, less so than abdomen; compound eyes greatly reduced, rudimentary, appearing as depressions behind antennae; ocelli absent; antennal bases widely separated, inserted in deep frontal pits; scape hidden in pit, pedicel and postpedicel setulose (Fig. 2); arista unsegmented (Fig. 2); setae below antennal pit curved anterodorsally; ptilinal fissure (Fig. 2) especially prominent, ending near each outer side of antennal pit, with internal wedge-shaped sclerotisation medially; face broad, slightly convex; gena narrow, with several stout bristle-like setae; frontoclypeal suture distinct; clypeus (Fig. 2) formed of distinct glabrous lobe; palpus broad, 1-segmented, large, flattened, slightly crescent-shaped, with long marginal setae.

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2021. Manual of Afrotropical Diptera. Volume 3. Brachycera—Cyclorrhapha, excluding Calyptratae. *Suricata* 8. South African National Biodiversity Institute, Pretoria; pp. 2289–2294.

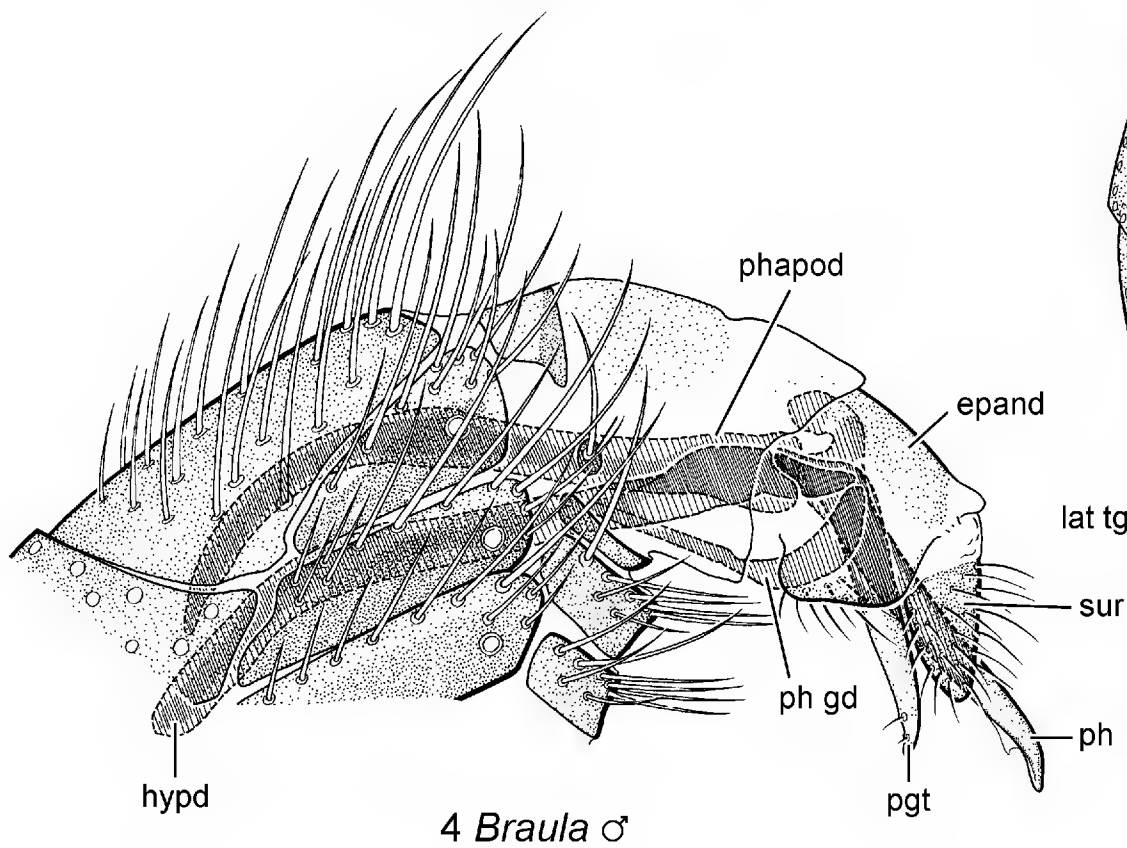
Thorax (Fig. 2) compressed, consisting of single mesonotal plate, shorter than head (viewed dorsally), without postpronotal lobes, wings, halters and scutellum (Fig. 2); mesopleural divisions very weak; epimeron reduced; mesothoracic spiracle large and apparent, situated high on anepisternum, appearing as crescent-like indentation; posterior spiracle small, with series of sensilla; postnotum greatly reduced, withdrawn; prosternum and proepisternum joined, forming precoxal bridge; posterior ½ of dorsum clothed in short setae, with row of long stiff setae on hind margin, 2–3 longer, stouter bristle-like setae at posterolateral corners, usually 2 similar bristle-like setae before mesothoracic spiracle. Legs (Fig. 2) stout, subequal in length, but relatively long in proportion to body size, with somewhat dense, long and short setae; femora with setae mostly on anterodorsal surface, with patch of long bristle-like setae on apicodorsal surface; femora bare on posterior surface; anteroventral and posteroventral margins with long setae; coxae broadly separated, with relatively large anterior coxae; tibia approximately equal in length to tarsus; all tarsi broadened apically; tarsomere 5 much wider than other four proximal



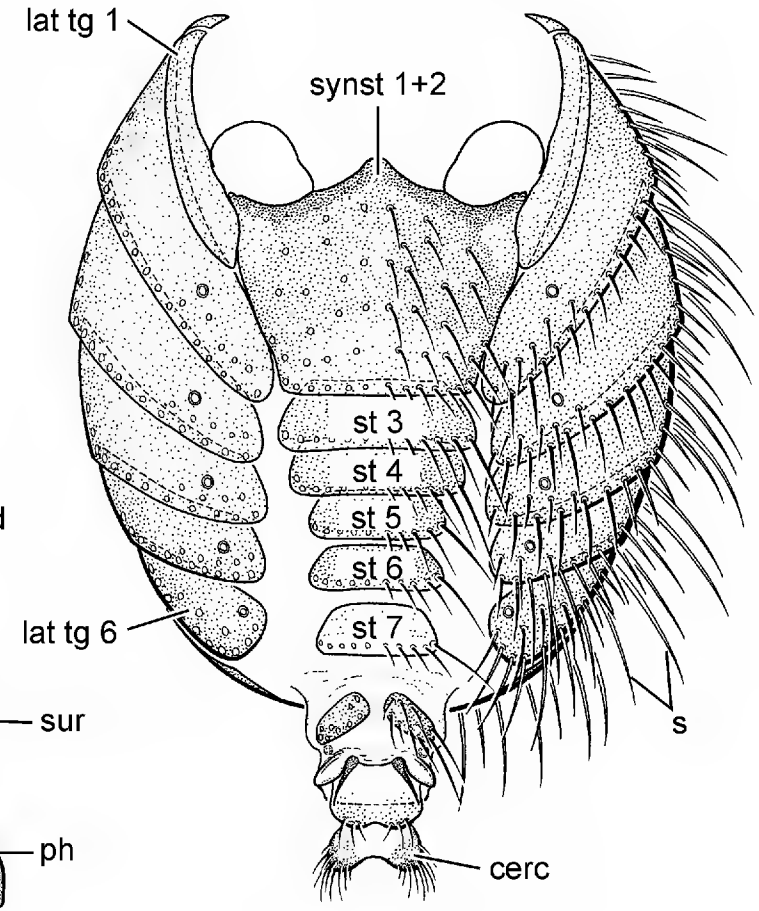
2 *Braula*



3 *Braula*



4 *Braula* ♂



5 *Braula* ♀

Figs 105.2–5. Habitus, tarsus, male terminalia and female abdomen of Braulidae: (2) habitus of *Braula coeca* Nitzsch ♀; (3) same, mid tarsus, ventral view; (4) same, male terminalia, lateral view; (5) same, female abdomen and terminalia, ventral view. Figs 2–5 (Peterson 1987, figs 1–4).

Abbreviations: ar – arista; cerc – cercus; clw – claw; clyp – clypeus; comp eye – compound eye; epand – epandrium; hypd – hypandrium; lat tg – lateral tergite; pgt – postgonite; ph – phallus; ph gd – phallic guide; phapod – phallapodeme; pped – postpedicel; ptil fis – ptilinal fissure; s – seta; st – sternite; sur – surstylus; synst – synsternite.

tarsomeres, triangular in shape, possessing pair of tarsal claws each modified into single-row toothed comb (Fig. 3).

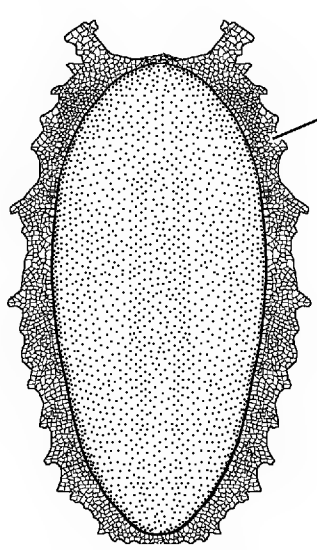
Abdomen (Figs 2, 5) short, broad, strongly convex, somewhat ovoid in outline, broadly attached to thorax (Fig. 5); both sexes with 5 visible tergites (syntergite 1 + 2; tergites 3–6); remaining segments usually withdrawn; tergites laterally expanded and subdivided into separate sclerites; both sexes with 5 visible sternites (when abdomen not extended), sternite 6 small, obscured in male; synsternite 1 + 2 as long, or longer than, combined length of remaining sternites; hind margins of tergites and sternites with long, stiff setae; male terminalia (Fig. 4) with stout, Y-shaped hypandrium, subequal in length to phallapodeme, open posteriorly; hypandrial bridge absent; gonopod situated at apex of hypandrial arm, separated by distinct suture; female terminalia (Fig. 5) with cercus small, distinct, fused medially with posteromedian emargination; cercal lobes rounded, setose (Fig. 4); 1 spermatheca present.

Egg (Fig. 6) white, broadly oval in shape, with one side somewhat less convex than other; surface of chorion finely reticulated, surrounded on sides by irregularly shaped flanges, possibly facilitating flotation in liquid honey to prevent freshly hatched larvae from drowning (Dobson 1999; Ferrar 1987: 82; Peterson 1987: 914).

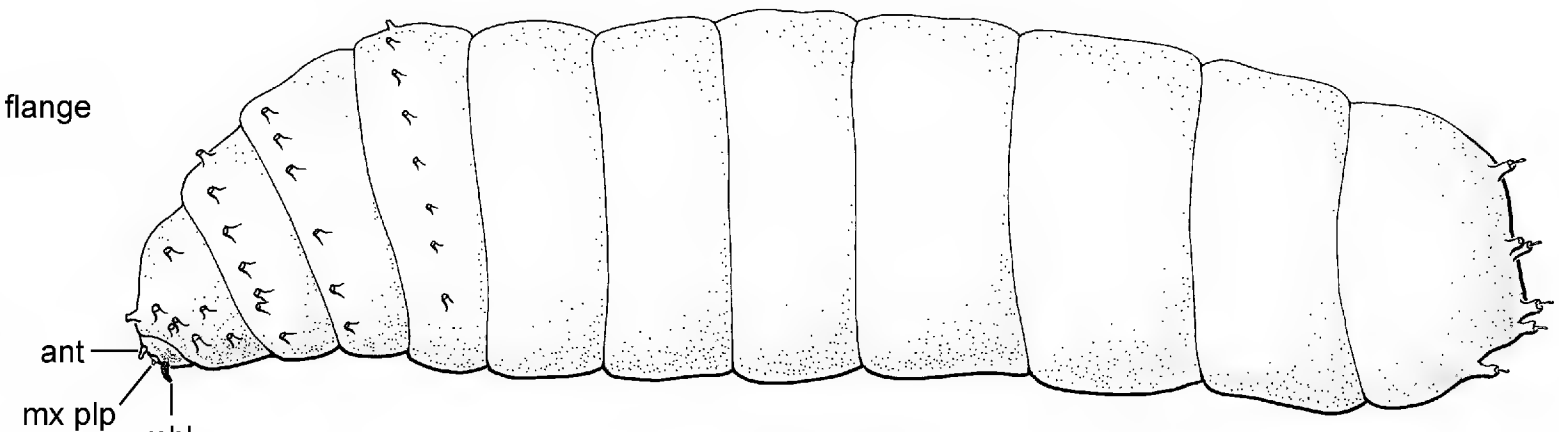
Larva (Fig. 7) with body cylindrical, tapered anteriorly, bluntly rounded posteriorly; all 3 instars similar morphologically; third-instar body similar to second-instar; cuticle appearing granulated; thoracic segments 1–3, abdominal segments 1 and 8 with girdled peg-like sensory structures (described in detail by Imms (1942)); cephaloskeleton (Fig. 8) amber coloured in all instars, but less sclerotised in first-instar than in others; mouthhooks distinctly shaped; dental sclerites absent; intermediate sclerite fused to basal sclerite; basal sclerite long, with slender dorsal and ventral cornua, approximately equal in size; without ventral cibarial ridges and parastomal bars; all instars without prothoracic spiracles; all three instars with posterior spiracular plates with sclerotised peritreme, 2 small oval spiracular openings present in first- and second-instars, arranged somewhat parallel and horizontal; third-instar posterior spiracles (Fig. 9) small, inconspicuous, with 3 small, virtually parallel spiracular openings on each spiracular plate.

Puparium creamy white in colour; *Braula* Nitzsch previously considered unique as pupa enclosed within unmodified cuticle of last larval instar; however, shape much contracted from larval shape, not unlike normal puparium with very thin walls, transparent and unsclerotised, possibly due to pupariation occurring within confines of larval tunnel; similar puparia found in Muscidae pupating inside of protective cocoons (Ferrar 1987: 83); larval head and first thoracic segments 1 and 2 form narrower constricted cap from rest of puparium (Ferrar 1987: 83).

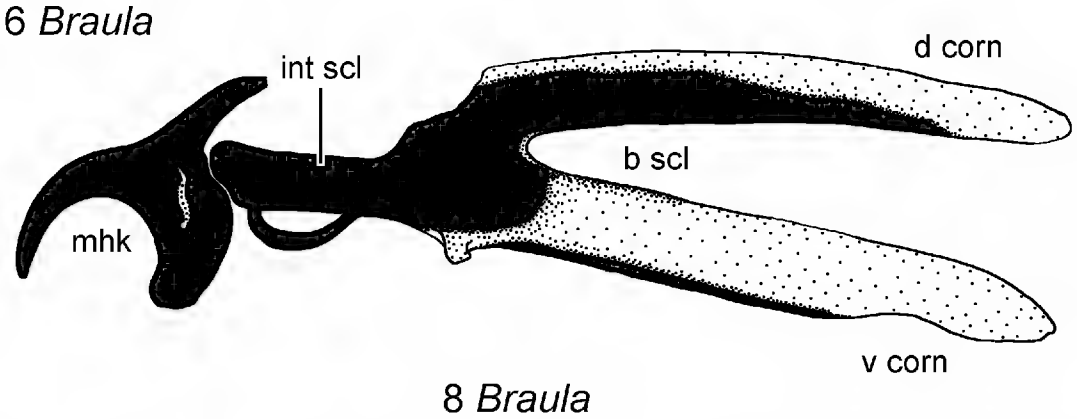
Adult braulids are unlikely to be confused with other Diptera families, due to their characteristic form and the situation in which they are found, although non-dipterists regularly misdiagnosed braulids in bee-hives as varroa mites, *Varroa*



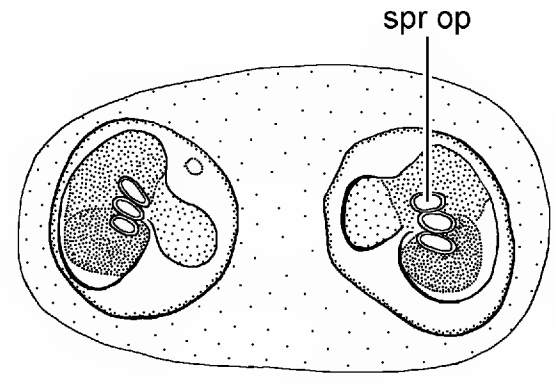
6 *Braula*



7 *Braula*



8 *Braula*



9 *Braula*

Figs 105.6–9. Immature stages of Braulidae: (6) egg of *Braula coeca* Nitzsch, dorsal view; (7) second-instar larval habitus, lateral view; (8) same, cephaloskeleton, lateral view; (9) third-instar larva, posterior spiracles. Figs 6, 8, 9 (after Imms 1942, figs 2, 4a, 7), Fig. 7 (Peterson 1987, fig. 5).

Abbreviations: ant – antenna; b scl – basal sclerite; d corn – dorsal cornu; int scl – intermediate sclerite; mhk – mouthhook; mx plp – maxillary palpus; spr op – spiracular opening; v corn – ventral cornu.

destructor Anderson & Trueman, due to their colour similarities and general shape.

Biology and immature stages

All species of *Braula* are kleptoparasites associated with honeybees and their hives. As adults are small and apterous, they cling to the bodies of workers or queens, although they have also been recorded on drones (Ferrar 1987: 81). They are typically found, singly, on the thorax or gaster area of the bee. Skaife (1922) reported that as many as 18 individuals have been recorded from a drone in South Africa, from a hive without a queen. Barton Smith & Caron (1984), however, reported as many as 29 on a single queen during field surveys from Maryland, U.S.A. They use their unique comb-like tarsal claws to grasp onto the setae of their hosts. Adults migrate to the head to feed on regurgitated material (typically protein and fat-rich secretions fed to the queen and larvae), from the bee's mouthparts, in response to stimulation by the fly (Dietz *et al*. 1971; Dobson 1999). Argo (1926: 172) described the stimulation as "frantically clawing" at the clypeus with the front tarsi, which induces regurgitation.

Adults occur in hives throughout the year, with the number of adults recorded differing throughout seasons across different regions (Strauss *et al*. 2014). Barton Smith & Caron (1984) noted that adults overwinter within bee colonies, with a marked increase in the mortality of females occurring in spring following oviposition.

Females oviposit in different locations within the hive, including empty cells, brood cappings, debris on the floor, but only eggs deposited on capped honey combs will hatch (Ellis *et al*. 2016; Imms 1942; Somerville 2007). The newly hatched larva constructs an initial thread-like tunnel out of the inner surface of the wax capping, moulding the fragments into a tube. The tunnel becomes enlarged as the larva grows and the tube may eventually traverse multiple cells, allowing the larva to move back and forth between cells. It has been postulated that larvae feed on honey and pollen residues that are encountered while constructing such tunnels (Ellis *et al*. 2016).

Pupariation occurs within the larval tunnel, which provides a safe shelter and compensates for the unsclerotised nature of the puparium. Just prior to pupariation, the larva cuts a fine circular groove on the inner wall of wax of the puparial chamber, allowing the newly eclosed adult to lift the wax operculum and exit the cell (Ferrar 1987: 82).

Immature stages of Braulidae have been described by Arnhart (1923), Ferrar (1987: 82), Hassanein & Abd El-Salam (1962), Hennig (1938, 1958), Imms (1942), Örösi-Pál (1938), Peterson (1987: 916) and Skaife (1922).

Economic significance

Braula are not considered to be of economic significance. Matheson (1993), and subsequently Ellis & Munn (2005), included *Braula* in their reports on worldwide honeybee health status, with Matheson (1993) stating that while it is not considered a parasite of honeybees, it is still an issue for some certifying authorities. It is typically considered an inquiline within hives (Peterson 1987: 916). The main potential impact that braulids have are that the wax-lined tunnels of the larvae spoil the appearance of honeycombs intended for show or sale (Dobson 1999).

Classification

Classification of the Braulidae has long been problematic, with their closest relatives having been initially postulated as the Phoridae, but later dipterists, such as Schmitz (1917) placed the family in the acalyptrates, due to the well-developed ptilinal fissure. Peterson (1987: 916) gave a comprehensive historical overview of the classification of the family and considered the Braulidae to be an "… isolated specialised family possibly allied to the Carnidae." Imms (1942) postulated that Braulidae is closely related to the Chamaemyiidae, due to larval structure, although Hennig (1952: 325) found the evidence unconvincing. Speight (1969) suggested an isolated position in the Acalyptratae, or even in the Drosophiloidea. Griffiths (1972: 218) treated the Braulidae as "families of uncertain relationship" and rejected the view of Hennig (1938, 1973) that *Braula* belongs to the Sphaeroceridae as well as the intermediary view of Hennig (1958) that the family might belong in Milichioidea and Drosophiloidea. Griffiths (1972: 218) suggested that Braulidae is closely related to the Lonchaeoidea and Lauxanioidea, and if not, should be referred to a separate monobasic superfamily. Rohdendorf (1974: 122) later suggested that Braulidae occupy its own infraorder, the Braulomorpha. This would, however, discount its affinities to the Acalyptratae, such as the aforementioned presence of the ptilinal fissure. Cogan (1980: 627) mentioned the relationship to be inconclusive. McAlpine (1989: 1471) placed the Braulidae in the superfamily Carnoidea and noted that all authors who have dealt with them placed them differently. Wiegmann *et al*. (2011) presented the most complete phylogeny of Diptera to date, based on molecular analyses and interestingly recovered Braulidae (together with Cryptochetidae) as sister-group to the Drosophilidae, within the superfamily Ephydroidea.

Two genera are recognised: *Braula*, which has a virtually cosmopolitan distribution, and is associated with honeybees, *Apis mellifera* L. and *Megabraula* Grimaldi & Underwood, which occurs in Nepal and is associated with *Apis laboriosa* Smith (Grimaldi & Underwood 1986).

Identification

Örösi-Pál (1966*a*) discussed *Braula* species and provided characters for each of the species-groups: *B. coeca*-group (comprising *B. coeca* Nitzsch, 1818); *B. pretoriensis*-group (comprising *B. kohli* Schmitz, 1914 and *B. pretoriensis* Örösi-Pál, 1938); *B. schmitzi*-group (comprising the non-Afrotropical *B. orientalis* Örösi-Pál, 1963 and *B. schmitzi* Örösi-Pál, 1939). Since his work, the only additional species description is that of *B. hansruttneri* Hüttinger, 1980, from the Palaearctic Region, which has since been synonymised with *B. coeca* (Evenhuis & Pape 2019; Hüttinger 1980; Papp 1998: 328). Dobson (1999) reviewed the Braulidae of the British Isles where he described and illustrated terminalia characters diagnostic for males of *B. coeca* and *B. schmitzi*. In addition he provided notes (based on the identification key and illustrations of Örösi-Pál (1966*b*)), to facilitate identification of some species known from the Afrotropical Region, that could potentially occur in the United Kingdom. Braulidae are best point-mounted (see Chapter 2).

Synopsis of the fauna

***Braula* Nitzsch.** A genus of five described species occurring in all zoogeographical regions, except Antarctica. Three species occur in the Afrotropical Region: *B. coeca* (with two subspecies: *B. coeca sensu stricto* and *B. coeca angulata* Örösi-Pál, 1966), recorded from Angola, Benin, Democratic Republic of Congo and Southern Africa; *B. kohli*, described from Democratic Republic of Congo; and *B. pretoriensis*, recorded from Democratic Republic of Congo, Mauritius (also on Rodrigues Is.), South Africa and Tanzania. *Braula coeca sensu stricto* is virtually cosmopolitan and *B. coeca angulata* has been recorded from Italy in the Palaearctic, as an introduced species (Dobson 1999). The genus is exclusively associated with adult honeybees and their hives (Dobson 1999). *Braula coeca* is the only species of the genus that has had its immature stages described. Afrotropical species can be identified by reference to Örösi-Pál (1966*b*) and Dobson (1999).

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DROSOPHILIDAE 106

(Ferment Flies, Vinegar Flies or Fruit Flies)

Shane F. McEvey and David A. Grimaldi

Fig. 106.1. Undetermined sex of *Drosophila* sp. (Tanzania) (photograph © S.A. Marshall).

Diagnosis

Small- to moderately sized (body length: 1.2–6.0 mm), stout-bodied to gracile acalyptrate flies; colouration highly variable from velvety and metallic black, to brown, yellowish, to dull and reflective silvery and whitish, unicolourous to highly maculated (Figs 1–18); many groups without sexual dimorphism in colour, some dramatically dimorphic (e.g., *Leucophenga* Mik); wings hyaline, infuscate or patterned (Figs 50–63).

Head with 2–3 pairs of fronto-orbital setae; invariably with proclinate and posterior reclinate fronto-orbital setae; anterior reclinate fronto-orbital seta always smaller, sometimes minute or absent (Figs 23, 29, 38); face flat, or with vertical carina of variable development: long or short (not reaching oral margin), shallow or nose-like, margin rounded or flat, with or without median sulcus (Figs 64, 65); antenna with pedicel with dorsolateral cleft; postpedicel largest antennomere, suspended beneath pedicel (Fig. 21) or (rarely) projecting forward, with fine setulae, short (Fig. 26) to long (Fig. 21); arista with minute, ring-like basal article, rest of arista long, varying from bare and flagellate, to pubescent, to plumose (Figs 40–49); plumose arista always with dorsal branches and usually with at least one ventral branch (dorsoventral asymmetry in *Allopygaea* Tsacas, Fig. 40); branch lengths and number variable (Figs 40–49); ocellar setae well-developed (Figs 26, 27, 65); postocellar setae large (Figs 20, 64) to small (Fig. 66), parallel to cruciate; inner (medial) and outer (lateral) vertical setae well-developed,

inner vertical setae convergent (inclinate), outer vertical setae divergent (lateroclinate) (Figs 20, 28–30); frons with margins of ocellar triangle well- to poorly defined (Fig. 19); frons glabrous and shiny to dull/pruinescent (Figs 64–66); compound eye invariably large, bare to densely micropubescent (ommatrichia), unicolourous reddish to red-brown, sometimes with bands, patterns, or iridescence in living flies (Figs 22–39); eyes never holoptic or with dorsoventral facet differentiation (Figs 64–66); gena deep (Figs 28, 29) to very shallow (Figs 23, 39), with 1 (Fig. 27) or 2 (Figs 20, 34) pairs of vibrissae; proboscis always

Figs 106.2–7. Photographs of living Afrotropical Drosophilidae: (2) *Drosophila* sp. (Tanzania); (3) female *Leucophenga* sp. (Tanzania); (4) male *Leucophenga* sp. (Tanzania); (5) male *Leucophenga* sp. (Tanzania); (6) *Zaprionus* (*Z.*) *indianus* Gupta (South Africa); (7) *Zaprionus* sp. assembled on a leaf near fermenting fruit (South Africa). Figs 2–5 (photographs © S.A. Marshall), Fig. 6 (photograph © J.M. Herrera), Fig. 7 (photograph © H. de Klerk).

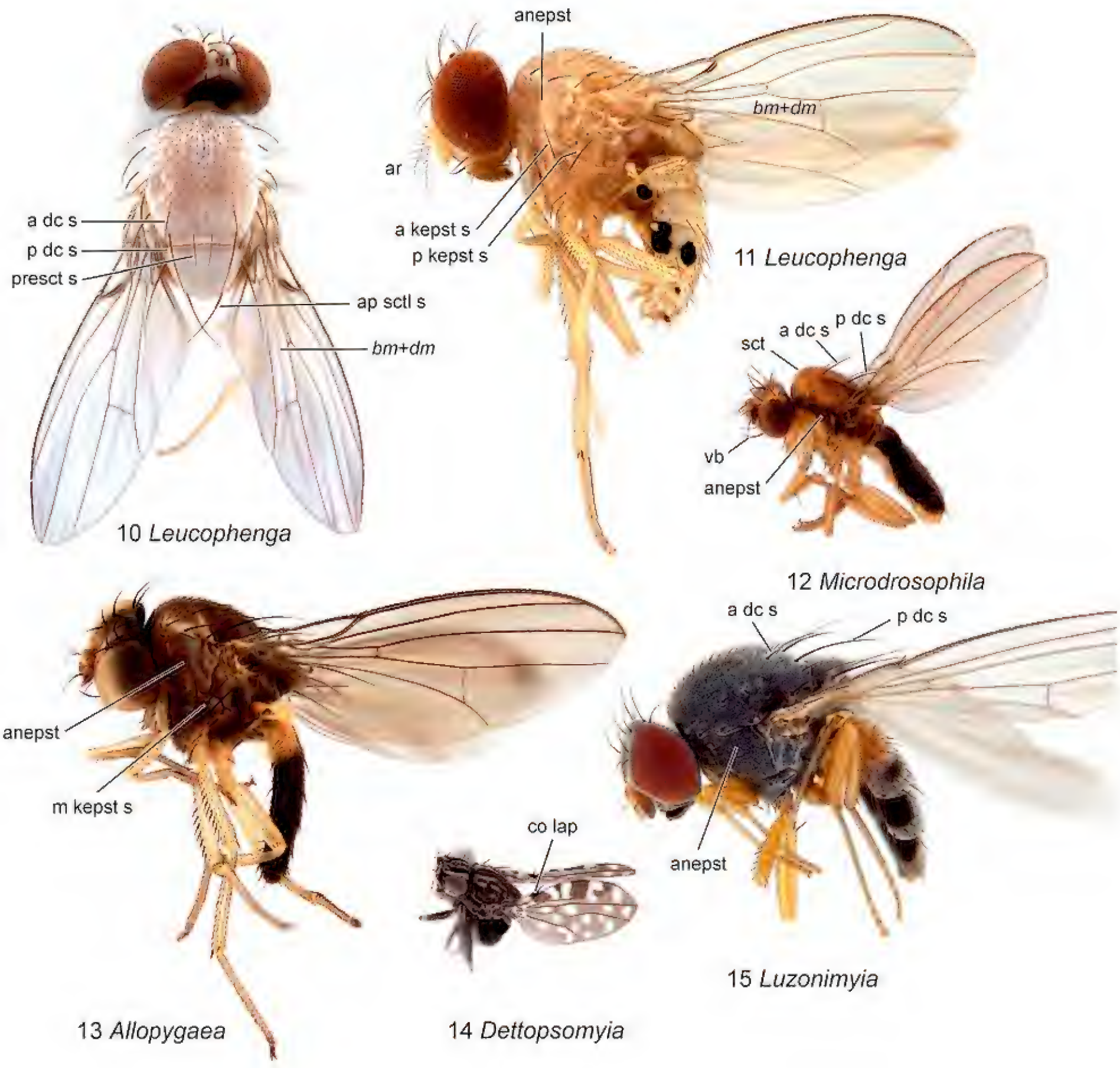
well-developed, visible when retracted into oral cavity, occasionally with long, slender prementum (theca); labellum small and barely broader than labium to much broader; palpus always developed, sometimes very large (hypertrophic).

Thorax of various colours and patterns; unicolourous, striped, freckled, or mottled (Figs 6–10, 14, 71–73); invariably with 1 large pair of dorsocentral setae, usually with 2 pairs (Fig. 19), rarely with additional pairs of small dorsocentral setae anterior to these; prescutellar setae present in all Steganinae (Fig. 68) and some Drosophilinae; acrostichal setae usually in even rows between anterior dorsocentral setae, varying from 2–12 rows (Fig. 19); postpronotum with 1–3 large postpronotal setae (Fig. 19); 2–3 notopleural setae (Fig. 19); 1–3 large katepisternal setae (Fig. 11); anepisternum invariably bare (Figs 11–13, 15) (or very rarely, with several small fine setulae centrally). Scutellum almost always with only 2 pairs of large scutellar setae (Fig. 19); apical scutellar setae parallel to cruciate (Figs 10, 19, 71–73); scutellar disk bare (Fig. 19), rarely setulose (e.g., *Paraleucophenga* Hendel). Wing fully developed in all but one brachypterous species (*Scaptomyza* (*Parascaptomyza*) *frustulifera* (Frey, 1954), from Tristan da Cunha Is.); costal vein (*C*) with humeral and subcostal breaks (Fig. 52), some groups with darkened, thickened costal lappet above subcostal break (Figs 17, 18, 50, 55); subcostal vein (*Sc*) incomplete (Figs 50, 54); costal vein (*C*) ending at apex of vein M_1 (Figs 50, 55); thick costal spinules ending between apices of veins R_{2+3} and R_{4+5}, this sector with black, thorn-like spinules in some Steganinae (Fig. 67); vein R_1 short (Fig. 50); length of vein R_{2+3} highly variable (Figs 18, 54), occasionally sinuous or (in *Jeannelopsis mirabilis* Séguy, 1938), with auxiliary veins between it and costal vein (Fig. 58); vein R_{4+5} ending at wing tip or very near tip (Fig. 50); vein M_1 parallel to (Figs 52, 54), or converging apically (Fig. 51) with vein R_{4+5}; crossveins *r–m* and *dm–m* invariably present (Figs 51, 54); crossvein *bm–m* sometimes weakly developed (Fig. 51); anal lobe and vein *CuA+CuP* highly variable, from well-developed (Figs 51, 54) to virtually lost (Fig. 55); alula always present, with fringe of long setae (Fig. 54); colouration of wing membrane varying from entirely hyaline (Fig. 54) to ornately patterned (Figs 52, 55, 56, 58, 62). Legs with fore leg most variable; fore femur ventrally with various spine-like setae in both sexes of some groups (e.g., *Drosophila* (*Drosophila*) *nasuta* Lamb, 1914, Fig. 74; *Zaprionus* (*Z.*) *vittiger* Coquillett, 1902, Fig. 70); terminal tarsomeres with black, spine/comb-like structures in some groups (e.g., *Drosophila suma* Burla, 1954; discussed in detail by Grimaldi & Jones 2020) and in males of many *D.* (*Sophophora* Sturtevant) species (e.g., *D.* (*S.*) *melanogaster* Meigen, 1830); many Afrotropical *D.* (*Sophophora*) species illustrated by Bock & Wheeler (1972), Burla (1954) and Tsacas & Chassagnard (1992); terminal tarsomeres with brushy ventral surfaces in some groups (e.g., *Drosophila* (*Drosophila*) *immigrans* species-group and *Zaprionus* Coquillett); males of many *Drosophila* Fallén with fine erect setulae on dorsal surface of terminal tarsomeres.

Abdomen with 6–7 pregenital tergites; male with tergite 8 lost; tergite 9 always well-developed as sub-hemispherical capsulate epandrium (Figs 75, 77); female with tergite 8 (sometimes reduced to small dorsolateral sclerites); spiracles of both sexes always in membrane, never in lateral portions of tergites (Figs 79, 82); males of some taxa with tergite 1 small, partially fused with tergite 2; spiracle 1 lost; male terminalia (Figs 75–78) highly diagnostic for species and species-groups, including genera; epandrium well-developed, with or without setae and microtrichia (Figs 75, 77); ventral lobes present or absent, sometimes large, with elaborate fringes of long setae (Fig. 75); ventral lobe of epandrium sometimes with smaller, medial accessory lobe; cercus always setose (Figs 75, 77), ventral margin sometimes with spines or denticles, sometimes distended into ventral lobes; cercus usually free; sometimes attached laterally to epandrium (e.g., *Drosophila virilis-repleta* "radiation"); surstyli almost always present (Figs 75, 77), usually articulating with epandrium proximally (sometimes fused), highly variable, simple, setose lobes or bearing tooth-like prensisetae (Fig. 75); subepandrial sclerite beneath cerci, articulates laterally with surstyli (Figs 75, 77); hypandrium (sternite 9) usually well-developed (Figs 75, 77); dorsal "arch" or hood-like structure sometimes present, lying above phallus and articulating with posterolateral arms of hypandrium; phallus extremely variable in length, shape and fine structure, particularly distiphallus

Figs 106.8–9. Photographs of living Afrotropical Drosophilidae: (8) *Jeannelopsis* sp. (South Africa); (9) *Mycodrosophila* (*Mycodrosophila*) sp. (South Africa). Figs 8, 9 (photographs © S.A. Marshall).

(Figs 75, 77, 78); paraphysis (*sensu* McAlpine 1981: 45), probably postgonite (*sensu* Cumming & Wood (2017: 129), usually simple pair of lobe-like structures flanking base of phallus (Figs 75, 77, 78); phallapodeme usually keel-like, sometimes plate-like, size and shape variable (Figs 75, 78); ejaculatory apodeme generally shaped like mason's palette (Fig. 76), flat surface lying against anterior surface of sperm sac; female terminalia (Figs 79–86) in early branching groups (*i.e.*, Steganinae, some Drosophilinae) with sternite 8 unmodified, or as small pair of simple sclerites; in most Drosophilinae sternite 8 modified into oviscape, comprised of 2 large lateral valves joined by thin anterior bridge (Figs 79, 82); ventral and apical



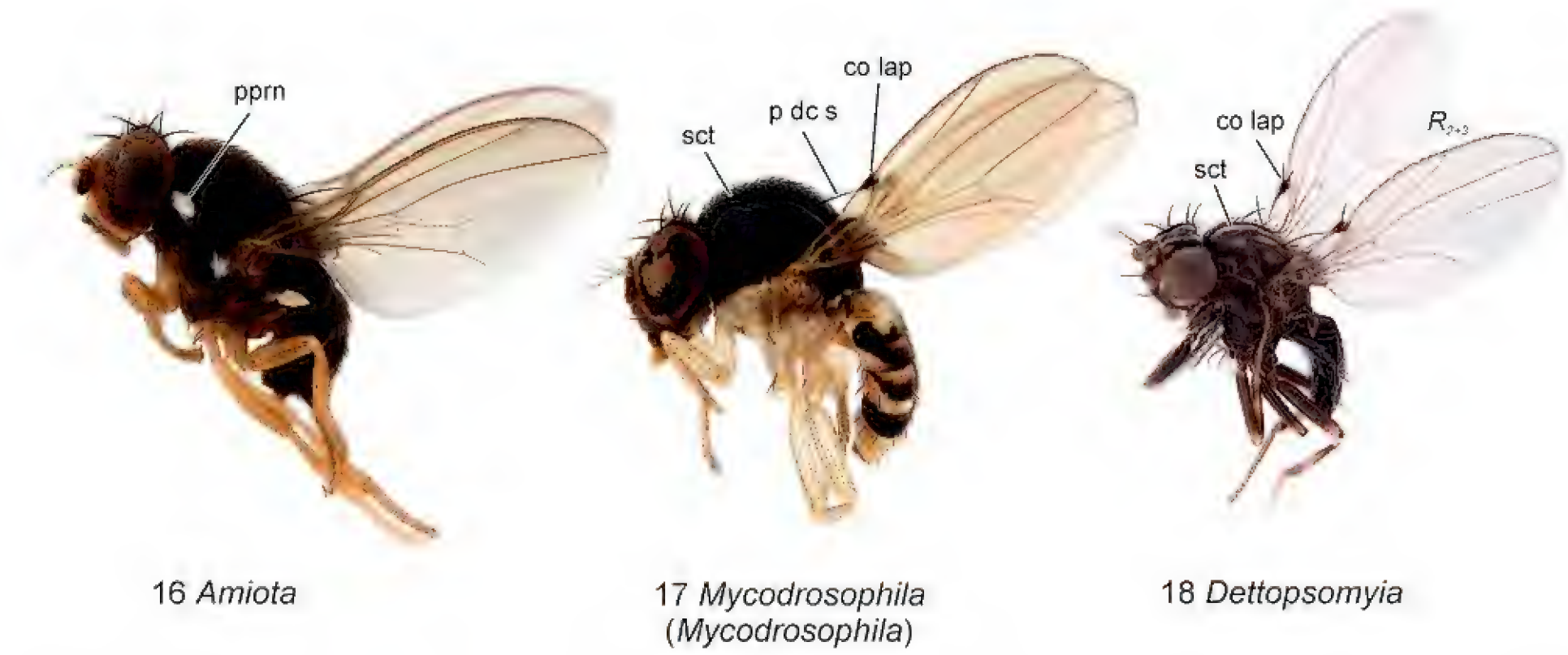
Figs 106.10–15. Habitus of Drosophilidae: (10) *Leucophenga perargentata* Bächli, dorsal view; (11) same, lateral view; (12) same, *Microdrosophila* sp.; (13) same, *Allopygaea* sp.; (14) *Dettopsomyia formosa* Lamb, dorsolateral view; (15) *Luzonimyia* sp., lateral view.

Abbreviations: a dc s – anterior dorsocentral seta; a kepst s – anterior katepisternal seta; anepst – anepisternum; ap sctl s – apical scutellar seta; ar – arista; *bm+dm* – basal medial cell + discal medial cell; co lap – costal lappet; m kepst s – medial katepisternal seta; p dc s – posterior dorsocentral seta; p kepst s – posterior katepisternal seta; presct s – prescutellar seta; sct – scutum; vb – vibrissa.

margins of valves commonly with tooth-like pegs (Figs 83, 86); structure of oviscape highly variable (Figs 79, 82); cerci present in some genera, but usually lost with enlargement of epiproct (Figs 79, 82) (Grimaldi 1990*a*); 1 pair spermathecae present; spermatheca forming sclerotised capsule (Figs 84, 85) or short tube (Fig. 80), lost in a few groups; structure highly variable; sclerotised ventral receptacle, found in some other ephydroids, absent.

Egg (Figs 87–96) ovoid, invariably whitish; micropyle nipple-like at anterior apex; Drosophilinae with 0–12 slender, subapical filaments near micropyle (Figs 88–96), none in Steganinae (Fig. 87) (micropyle and filaments of oviposited egg protrude from substrate); chorion always with some fine microsculpturing, in form of irregular hexagonal cells (imprints of follicle cells) (e.g., Fig. 94, inset); chorion ultrastructure variable (Kambysellis 1993), that of *Lissocephala disjuncta* Tsacas & Chassagnard, 1978, uniquely rugose in part (Fig. 89) (Tsacas & Lachaise 1979); Steganinae usually with finely striate longitudinal groove, having low flap along each lateral margin (Fig. 87); early branching drosophilines either without filaments (e.g., Figs 88, 89) or with generally 3–6 pairs (e.g., *Chymomyza* Czerny, Fig. 90, *Scaptodrosophila* Duda and the Neotropical genera *Cladochaeta* Coquillett and *Diathoneura* Duda); some genera with very shallow longitudinal groove (Figs 90, 91); *Microdrosophila* Malloch with 1 central filament (3–4 × length of egg in some cases, Fig. 96), or with 1 pair very close to micropyle; higher drosophilines typically with 1 or 2 pairs of filaments; *Scaptomyza* Hardy with filaments absent or present as 1–2 pairs of short stubs (Fig. 91); *Lordiphosa* Basden and *Drosophila* (*Sophophora*) with 1 subapical pair of filaments, flattened in many of the latter (Fig. 93); genera with 2 pairs of filaments (Figs 92, 93, 95) include, e.g., *Dettopsomyia* Lamb, *Dichaetophora* Duda, *Drosophila*, *Hirtodrosophila* Duda, *Liodrosophila* Duda, *Zaprionus* and *Zygothrica* Wiedemann; *Mycodrosophila* Oldenberg with 1 or 2 filament pairs (if 2, then more apical pair shorter); exceptions in *Drosophila* include the *D.* (*D.*) *quinaria* species-group (with 3 filaments) and *D.* (*D.*) *melanica* species-group (with 1 pair) (both groups Holarctic) and a few others; egg filaments in some *Drosophila* forked at tips; species developing in flowers typically lay few eggs with highly reduced or no filaments.

Larva (Fig. 97) typically schizophoran; form maggot-like with 3 larval instars; respiratory system amphipneustic; body rarely with tubercles (e.g., *Drosophila* (*Dorsilopha*) *busckii* Coquillett, 1901, Fig. 99) or other ornamentation; pseudocephalon externally with typical array of fringed, oral lamellae; maxillary palpus and antenna papilla-like (Grimaldi & Nguyen 1999, fig. 170); cephaloskeleton (Fig. 103) invariably sclerotised; mouthhooks always well-developed (Figs 103–106), highly varied in dentition of ventral margin, from smooth (Fig. 108) to finely serrate (Fig. 104), or with spine-like teeth (Figs 105, 106); *Microdrosophila* uniquely with teeth at apex; Afrotropical species predatory on blackfly larvae and dragonfly eggs with stout, untoothed mouthhooks fused dorsally (Fig. 108; Tsacas & Disney 1974); first-instar larva lacking epistomal sclerite ("epipharyngeal" *sensu* Okada 1968) and H-shaped intermediate sclerite (Fig. 103), parastomal bar and dorsal bridge (Fig. 103), these always well-developed in third-instar larva, with dorsal bridge always fenestrated; thorax and abdomen ventrally with irregular, transverse rows of creeping welts (Fig. 97); New World genus *Cladochaeta* and the Afrotropical species *Leucophenga proxima* (Adams, 1905), with pair of prolegs on each of abdominal segments 6–8, each proleg with crown of crochets developed from creeping welts (both taxa feed on nymphal hemipterans (Grimaldi & Nguyen 1999; Medler & Adenuga 1969)); spiracular papillae of prothoracic spiracle partially everted, multibranched, highly variable in number and lengths (Figs 100–102); pair of posterior spiracles (Figs 97–99) never fused along



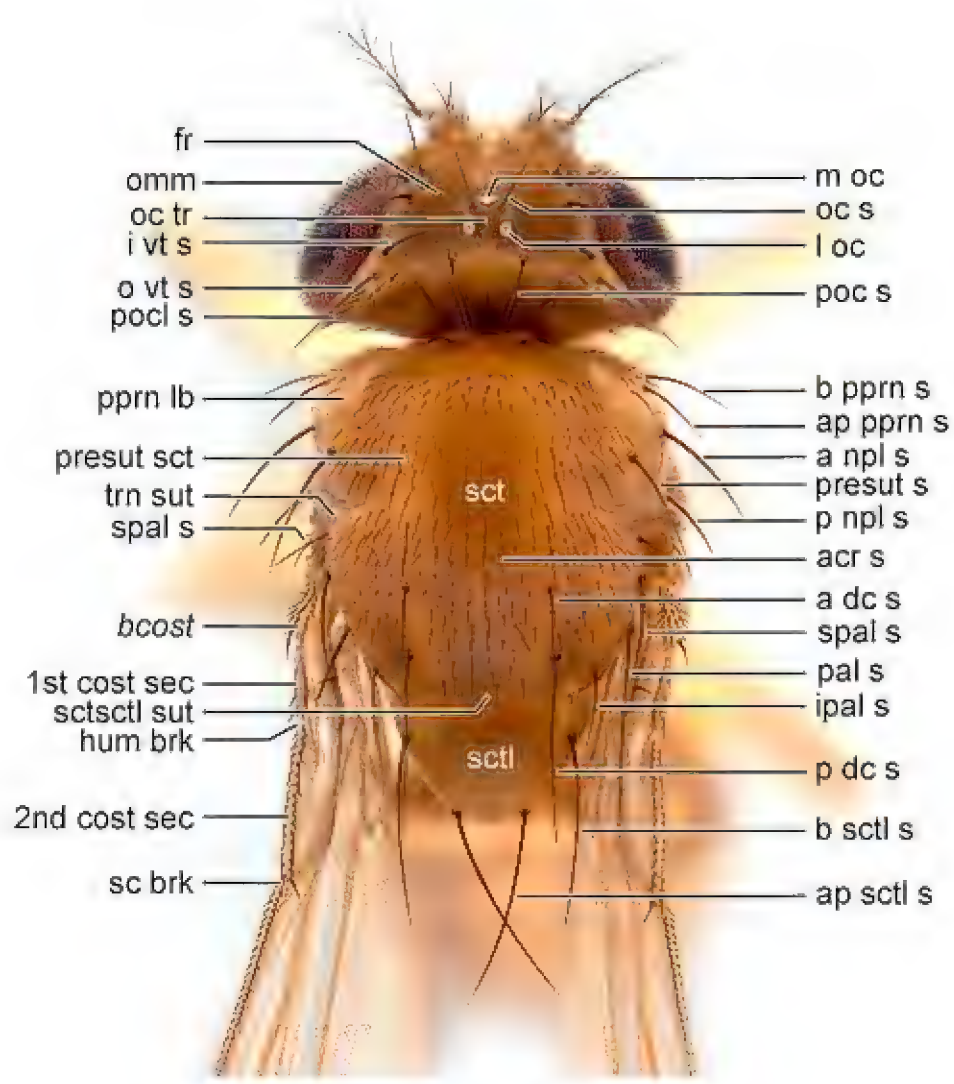
Figs 106.16–18. Habitus of Drosophilidae: (16) *Amiota albomaculata* (Duda), lateral view (non-Afrotropical); (17) same, *Mycodrosophila* (*Mycodrosophila*) *gratiosa* (de Meijere); (18) *Dettopsomyia nigrovittata* (Malloch), dorsolateral view.

Abbreviations: co lap – costal lappet; p dc s – posterior dorsocentral seta; pprn – postpronotum; R_{2+3} – second branch of radius; sct – scutum.

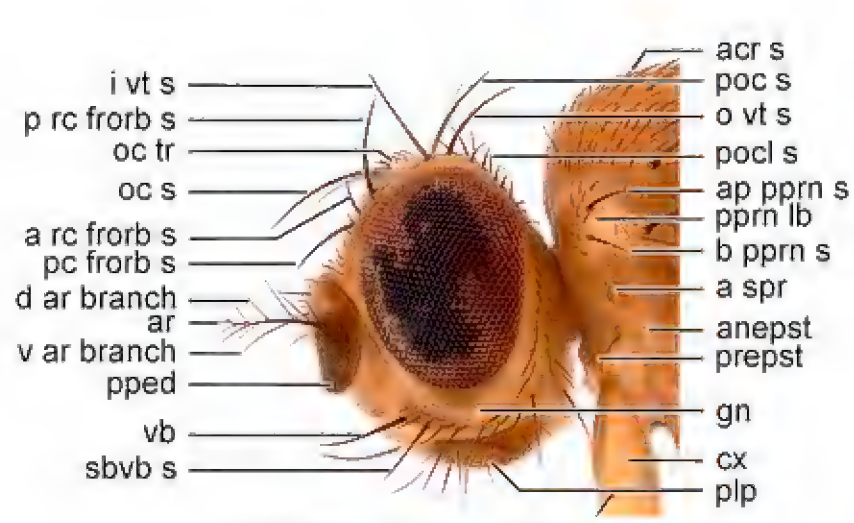
full length, short in many steganines, longer to very telescoping in some drosophilines (especially taxa in wet substrates); apex with lateral fringe of 4 branched, flattened peristigmatic tufts; posterior tubercles (Figs 98, 99) variable, least developed in predatory genera; anal pad best developed in saprophagous taxa; larvae of some Neotropical *Drosophila* curl and rapidly release, flinging themselves several centimeters.

Puparium (Figs 109–112) best described by Okada (1968) and Patterson (1943); formed from hardened third-instar larval cuticle, degree of melanisation varying from light (e.g., *Leucophenga*) to heavily sclerotised (some *Drosophila*); puparium cemented to dry substrate away from food source; ventral surface slightly to highly flattened; prothoracic spiracular papillae and base fully everted (Fig. 109, inset); length, number of papillae, length of base taxonomically varied; "horn-index", used widely, being ratio of lengths of prothoracic spiracle (papillae + base) divided by that of puparium: Steganinae always with very short base and few, short papillae; Drosophilinae with base short (early branching *Scaptomyza*), to longer than puparium (some *Drosophila*); prothoracic spiracular papillae from few (*ca* 8–12), these short in early branching genera (e.g., *Chymomyza*, Fig. 102), to long, fine, brush-like in some *Drosophila* (e.g., Fig. 100). *Drosophila* (*D.*) *simulivora* Tsacas & Disney, 1974, with nearly 100 such papillae; prothoracic spiracular papillae black in some *Hirtodrosophila* and *Zygothrica* where known.

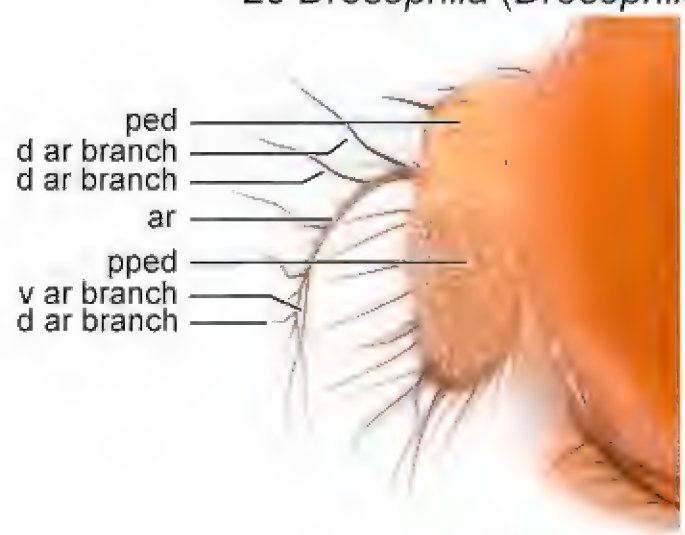
Drosophilidae are most often confused with other acalyptrates that have a plumose arista: some Ephydridae (see Chapter 100) and Lauxaniidae (see Chapter 74) and the families Camillidae (see Chapter 102), Curtonotidae (see Chapter 103), Diastatidae (see Chapter 104) and Periscelididae (see Chapter 91). Many Ephydridae have a bulging face and large



19 *Drosophila* (*Drosophila*)



20 *Drosophila* (*Drosophila*)



21 *Leucophenga*

Figs 106.19–21. Head, thorax, and antenna of Drosophilidae: (19) head and thorax of *Drosophila* (*Drosophila*) *funebris* (F.), dorsal view; (20) same, head, lateral view; (21) antenna of *Leucophenga paracapillata* Bächli, lateral view.

Abbreviations: a dc s – anterior dorsocentral seta; a npl s – anterior notopleural seta; a rc frorb s – anterior reclinate fronto-orbital seta; a spr – anterior spiracle; acr s – acrostichal seta; anepst – anepisternum; ap pprn s – apical postpronotal seta; ap sctl s – apical scutellar seta; ar – arista; b pprn s – basal postpronotal seta; b sctl s – basal scutellar seta; *bcost* – basicosta; cost sec – costal sector; cx – coxa; d ar branch – dorsal aristal branch; fr – frons; gn – gena; hum brk – humeral break; i vt s – inner vertical seta; ipal s – intrapostalar seta; l oc – lateral ocellus; m oc – median ocellus; o vt s – outer vertical seta; oc s – ocellar seta; oc tr – ocellar triangle; omm – ommatrichia; p dc s – posterior dorsocentral seta; p npl s – posterior notopleural seta; p rc frorb s – posterior reclinate fronto-orbital seta; pal s – postalar seta; pc frorb s – proclinate fronto-orbital seta; ped – pedicel; plp – palpus; poc s – postocellar seta; pocl s – postocular seta; pped – postpedicel; pprn lb – postpronotal lobe; prepst – proepisternum; presut s – presutural seta; presut sct – presutural scutum; sbvb s – subvibrissal seta; sc brk – subcostal break; sct – scutum; sctl – scutellum; sctsctl sut – scutoscutellar suture; spal s – supra-alar seta; trn sut – transverse suture; v ar branch – ventral aristal branch; vb – vibrissa.

clypeus; Lauxaniidae have two large pairs of reclinate fronto-orbital setae and no proclinate setae; Periscelididae have either one fronto-orbital seta (reclinate) or two (reclinate + interfrontal), the eyes are emarginate frontally and the costal wing vein (C) lacks both the humeral and subcostal breaks. The closely related ephydroid families Camillidae, Curtonotidae and Diastatidae all possess a ctenidium, a comb-like row of stout setae on the anteroventral surface of the apical portion of the fore femur (as do a few groups of drosophilids) (Fig. 74). In addition, in Curtonotidae the anepisternum and often the scutellum is setulose. In Camillidae and Diastatidae the antennal arista is long-pubescent to short-plumose and Camillidae also have lost wing crossvein *bm–m* and males have a large tergite 4. Diastatidae have large spinules on the costal wing vein (C) (as do some Curtonotidae) and the proclinate fronto-orbital seta is inserted posterolateral (instead of anterior) to the reclinate fronto-orbital seta. Drosophilidae with a pubescent or bare arista (Figs 42, 44, 46, 48) are best distinguished by the pair of proclinate fronto-orbital setae and two pairs of reclinate fronto-orbital setae (Figs 28, 29).

Biology and immature stages

Drosophilidae usually occur in places where desiccation stress is low – in damp shaded gullies and riparian vegetation and in habitats close to the ground, under forest logs, and shielded from direct sunlight and wind. Species found in more exposed habitats are usually living within flowers (where they aggregate as adults, court, mate and oviposit), or in other small spaces where humidity levels exceed ambient conditions. Many species are attracted to resources where yeasts and bacteria have initiated fermentation and rot of plant material, especially fruit and flowers, but also other soft plant tissues, sweet exudates and accumulations of partially digested or excreted plant fragments. Fungal growths are attractive to another cohort of drosophilid species, sometimes with ten or more mycophagous species in large numbers simultaneously exploiting a single fungal bloom or fructification; dry fungus is unattractive to drosophilids. Consequently, the most frequently successful collecting methods include fruit-baiting, Malaise trapping in shaded damp habitats, direct aspiration from fungus and flowers and sweep-netting over damp forest floors. The ease with which certain species of Drosophilidae (almost exclusively species of *Drosophila* and *Zaprionus*) can be established as living cultures in the laboratory is well-known. Cultures of some species have been held *in vitro* for decades. As a general rule the species attracted to fermenting fruit are the ones that can be bred easily in laboratories.

It is well-known that fermenting fruit in any equatorial rainforest globally will attract large numbers of drosophilid flies, but only in the Afrotropics is one likely to encounter large numbers of both *Drosophila* and/or *Zaprionus* species (Fig. 7) at fruit-baits. The abundance of *Zaprionus* in the continental Afrotropics and Madagascar is a distinctive component of the Afrotropical drosophilid fauna (47 species: 59 globally). *Leucophenga* is another well-represented genus in the Afrotropics (67 species), but is seldom collected at fruit (more often taken by random net-sweeping along forest paths or in Malaise traps) and males are often noticed because they display strong silvery pruinescence (Figs 5, 10, 11). The visibility of the pruinescence changes dramatically when a specimen is viewed at different angles (compare the same specimen shown at different angles in Figs 10 and 11) or when preserved in alcohol.

Lissocephala comprises 22 described species, each adapted to one or several species of *Ficus* (Moraceae). The radiation of this genus in the Afrotropics appears to be closely associated with the fig species in which they breed (Lachaise 1977). Such host-specificity is more the exception than the rule and many frugivorous drosophilids, especially species of *Drosophila* and *Zaprionus*, can be readily lured to rotting banana bait.

The immature stages of Drosophilidae are poorly studied compared to adults, even for laboratory cultured species of *Drosophila*. The most comprehensive study remains the classic monograph by Okada (1968), supplemented by various subsequent studies referenced below. Traditional taxonomic features concern the egg filaments (presence/absence and number) and prothoracic spiracles of the puparium (Burla 1954; Patterson & Stone 1952: 14; Sturtevant 1921: 18, 1942; Throckmorton 1962).

Economic significance

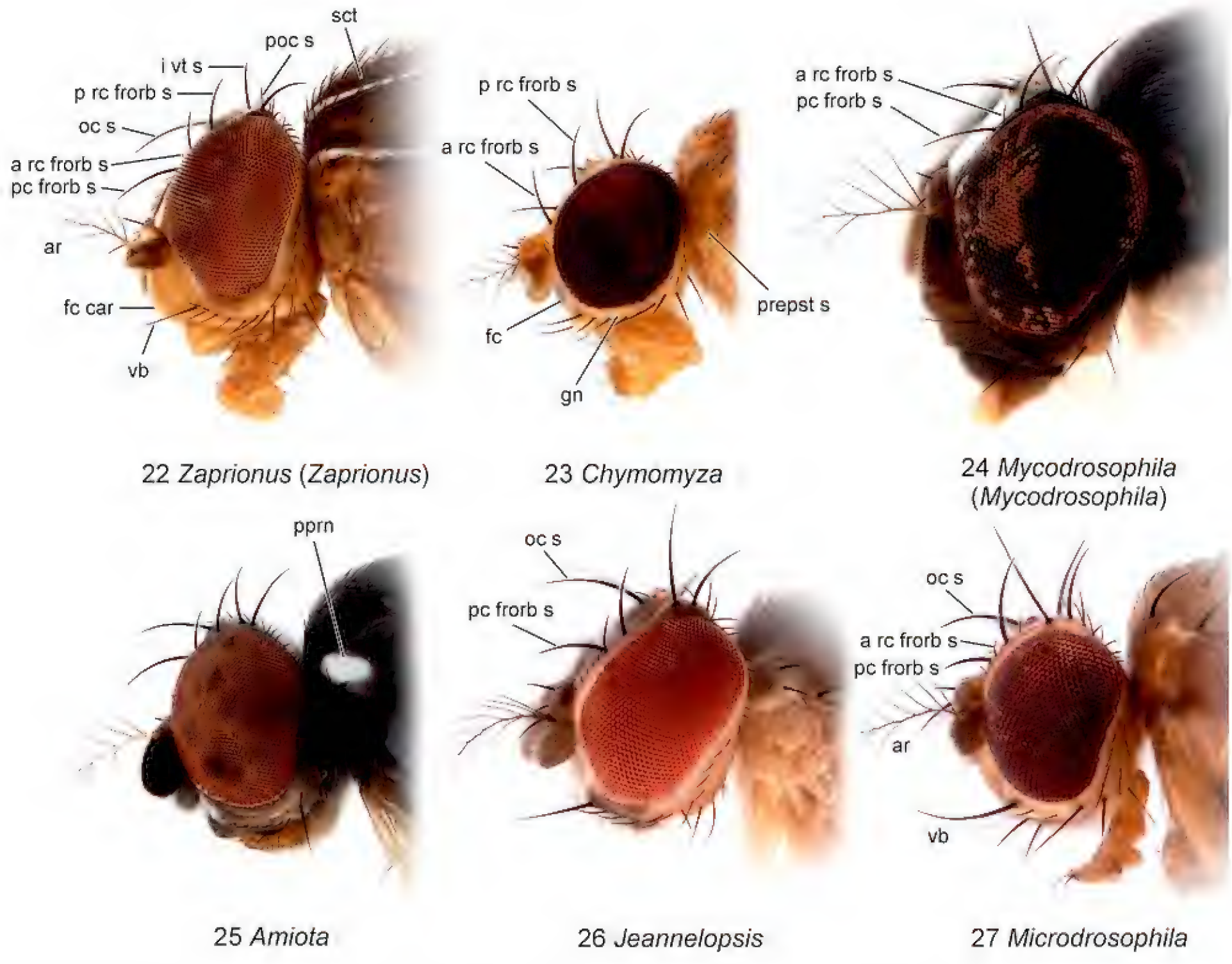
Together with malarial mosquitoes, there are few organisms that have impacted on human health as profoundly as *Drosophila* (*S.*) *melanogaster*: the culicid as vector of disease, the drosophilid as the most valued model organism in genetic and medical research. *Drosophila* (*S.*) *melanogaster* belongs to a group of nine morphologically very similar species, three of which are Afrotropical island endemics (*D.* (*S.*) *mauritiana* Tsacas & David, 1974, *D.* (*S.*) *santomea* Lachaise & Harry, 2000 and *D.* (*S.*) *sechellia* Tsacas & Bächli, 1981), two of which (*D.* (*S.*) *teissieri* Tsacas, 1971 and *D.* (*S.*) *yakuba* Burla, 1954) are widespread endemic Afrotropical species (Lachaise *et al.* 1988; McEvey 1990*b*) and two are either exceedingly rare (*D.* (*S.*) *orena* Tsacas & David, 1978, collected only once in the Cameroon Mountains), or highly specialised (*D.* (*S.*) *erecta* Tsacas & Lachaise, 1974, abundant only during the short *Pandanus* fruiting season in Côte d'Ivoire) (David *et al.* 2007). The remaining two species are among the most ubiquitous of all flies: *D.* (*S.*) *melanogaster* and *D.* (*S.*) *simulans* Sturtevant, 1919 (illustrated in McEvey 2017*a*), found in kitchens and peridomestic habitats globally, but most likely with an Afrotropical origin (Lachaise *et al.* 1988).

The significance of *Drosophila* research was outlined in the White Paper (*Drosophila* Board White Paper 2005: 1), as follows: "The powerful genetic manipulations built on a century of genetic research on *Drosophila melanogaster* with modern genomic technologies [has yielded] an unparalleled model for understanding animal biology. Further, the genus *Drosophila* has been an important model for understanding animal populations and evolution. The striking level of conservation of many genes, proteins and pathways between fly and human have ensured that *Drosophila* research is directly relevant to human disease, and indeed, the vertebrate biological community often looks to *Drosophila* research to identify candidate genes for pathways or diseases of interest, and to provide insights into the mechanisms underlying these vertebrate processes. Key insights have been gained in recent years into the genetic and cellular mechanisms of processes such as

neurodegeneration, vasculogenesis, the innate immune response, stem cell determination and maintenance, cell and tissue polarity, signal transduction, growth control, neural control of behaviour and organogenesis. In addition to insights gained for basic biology and human disease, *Drosophila* research also impacts on human health by serving as the closest genetic model for the insect vectors of disease, such as *Anopheles gambiae* (malaria), *Aedes aegypti* (dengue fever, yellow fever), *Culex pipiens* (West Nile fever), *Rhodnius proxilus* (Chagas disease) and *Glossina morsitans* (African sleeping sickness). It is now becoming clear that *Drosophila* research is producing the technologies and information sets that will inform genomic/genetic research in these medically important species, and that the *Drosophila* community is also likely to provide the training for future researchers in these species."

Wolbachia is an endosymbiotic intracellular bacterium present in about 60% of all insects, including some mosquitoes, but not *Aedes aegypti* (L.), the primary vector species for dengue virus. Advances in understanding the reproductive phenotype of *Wolbachia* infection have involved using *Drosophila* species as models (e.g., Richardson *et al*. 2019). Insights gained initially from many *Drosophila* studies ultimately led to effective dengue control. Transinfection of the *w*MelPop *Wolbachia* strain from *Drosophila* (*S*.) *melanogaster* to *Aedes aegypti* led to a 19% reduction in fecundity and an over 50% increase in adult mortality due to *w*MelPop infection in *Aedes aegypti* (Dorigatti *et al*. 2018).

Drosophila (*S*.) *flavohirta* Malloch, 1924 (Figs 31, 45) was first discovered in Australia from "flower sweepings". Until the



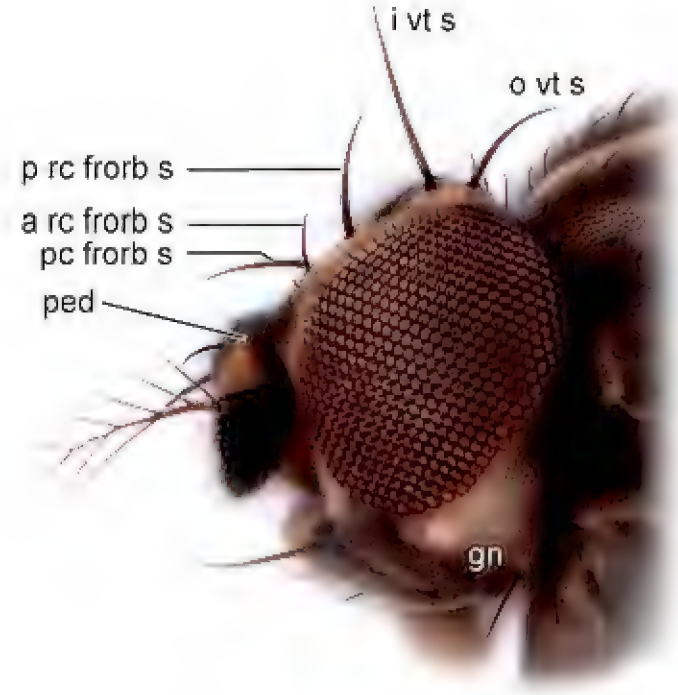
22 *Zaprionus* (*Zaprionus*) 23 *Chymomyza* 24 *Mycodrosophila* (*Mycodrosophila*)

25 *Amiota* 26 *Jeannelopsis* 27 *Microdrosophila*

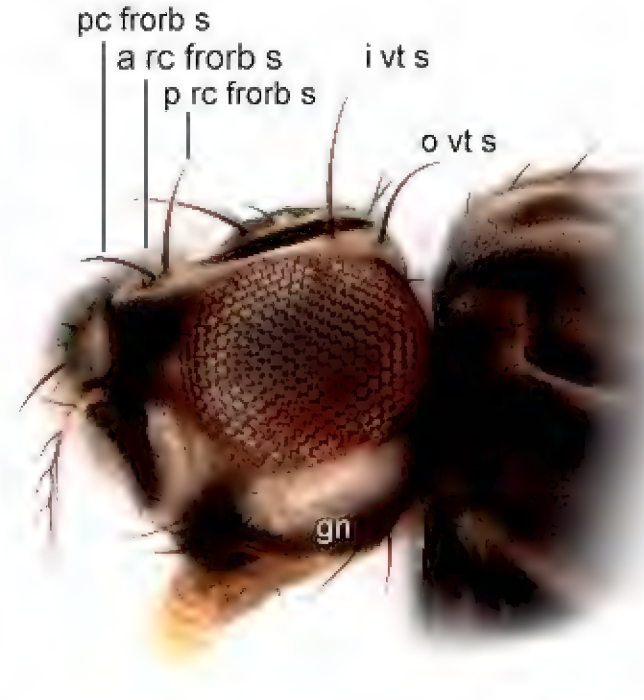
Figs 106.22–27. Heads of Drosophilidae (lateral views): (22) *Zaprionus* (*Z*.) *sexvittatus* Collart; (23) *Chymomyza bicolor* Lamb; (24) *Mycodrosophila* (*Mycodrosophila*) *gratiosa* (de Meijere); (25) *Amiota* sp.; (26) *Jeannelopsis zophoptera* Tsacas; (27) *Microdrosophila* sp.

Abbreviations: a rc frorb s – anterior reclinate fronto-orbital seta; ar – arista; fc – face; fc car – facial carina; gn – gena; i vt s – inner vertical seta; oc s – ocellar seta; p rc frorb s – posterior reclinate fronto-orbital seta; pc frorb s – proclinate fronto-orbital seta; poc s – postocellar seta; pprn – postpronotum; prepst s – proepisternal seta; sct – scutum; vb – vibrissa.

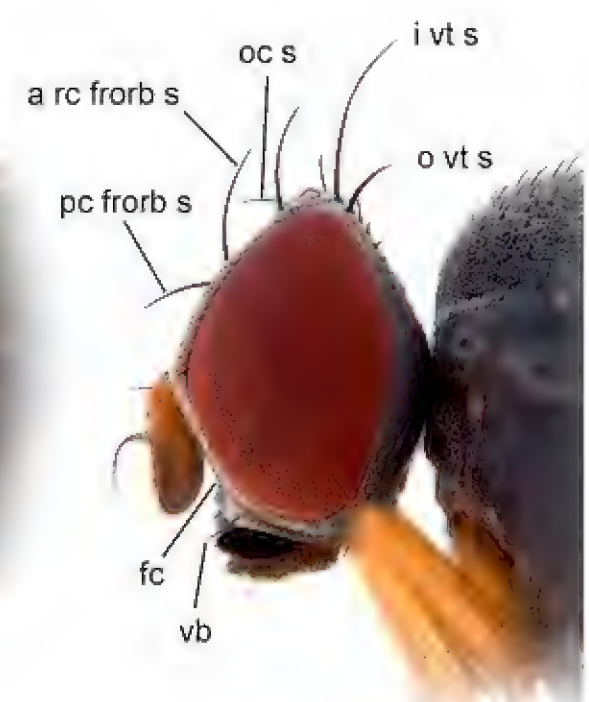
1980s, the species was poorly known and scant attention was given to their association with flowers. Living flies have small iridescent, red-green eyes and diffuse green banding on the abdominal tergites; they are not *Drosophila*-like in these respects and are easily confused with small similarly coloured chloropids that occur in the same habitats. Of the 26 specimens collected in Australia between 1923 and 1981, only the type specimens and one other had label information indicating anthophilic behaviour and in only one case was *Eucalyptus* (Myrtaceae) mentioned (Bock 1976). Nevertheless, when this species was identified as having a serious negative impact on honey yield in South African *Eucalyptus grandis* W. Hill (Myrtaceae) plantations (Buys 1983; du Toit 1987; Herrmann 1983, 1984), the conclusion was that, considering it being associated with *Eucalyptus* blossom, it had spread from Australia to the Afrotropics (McEvey *et al*. 1989). Furthermore, it appeared that in the absence of natural predators in the Afrotropics, its abundance had increased to pest status unabated. The flies' super-abundance on *Eucalyptus* blossom and the apparent absence of predators were lines of evidence that seemed to point to an Australian origin for this species. Further sampling in Southern Africa, Madagascar, South-east Asia and throughout Australia since 1981 has thrown a different light on the "Nectar fly" and its biogeography. Firstly, this species does in fact occur commonly on blossom in Australia (S.F. McEvey, pers. obs.; Tribe 1991), its apparent rareness was a mere artefact of collection method and focus. Collection method was also shown to be of importance when this species was recently



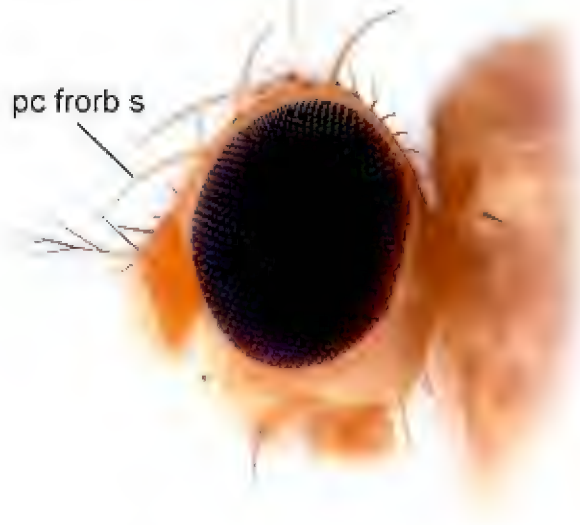
28 *Dettopsomyia*



29 *Dettopsomyia*



30 *Luzonimyia*



31 *Drosophila* (*Sophophora*)

32 *Stegana*

33 *Apenthecia*

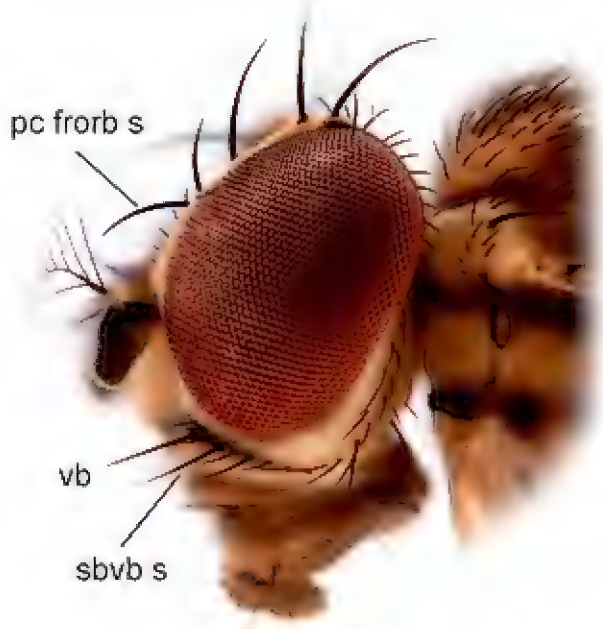
Figs 106.28–33. Heads of Drosophilidae (lateral views): (28) *Dettopsomyia nigrovittata* (Malloch); (29) *De. formosa* Lamb; (30) *Luzonimyia* sp.; (31) *Drosophila* (*Sophophora*) *flavohirta* Malloch; (32) *Stegana* sp.; (33) *Apenthecia* sp.

Abbreviations: a rc frorb s – anterior reclinate fronto-orbital seta; fc – face; gn – gena; i vt s – inner vertical seta; o vt s – outer vertical seta; oc s – ocellar seta; p rc frorb s – posterior reclinate fronto-orbital seta; pc frorb s – proclinate fronto-orbital seta; ped – pedicel; plp – palpus; vb – vibrissa.

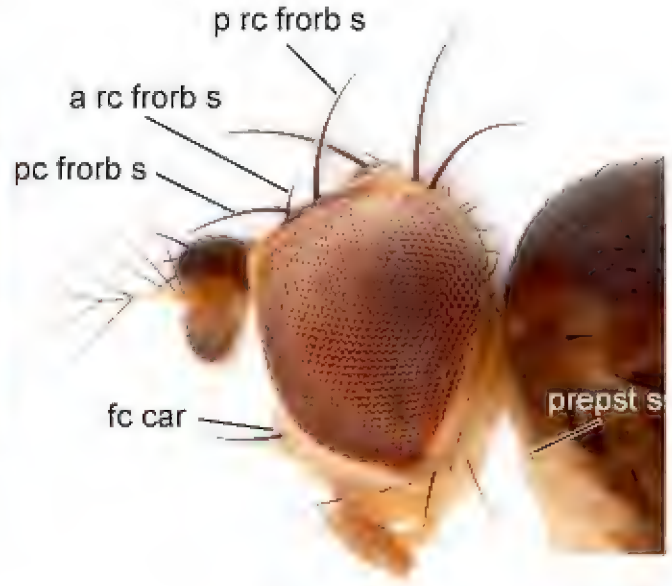
discovered in California, U.S.A. (Grimaldi *et al*. 2015). Secondly, and most importantly, *D*. (*S*.) *flavohirta* is abundant in blossom of other myrtaceous genera: *Angophora*, *Callistemon* and *Syzygium* (as *Eugenia* in McEvey *et al*. 1989) (Grimaldi *et al*. 2015). The large genus *Syzygium* is, unlike *Eucalyptus*, not naturally restricted to Australia. This means that *D*. (*S*.) *flavohirta* is not necessarily autochthonous Australian. *Syzygium* has some 1,200 species, ranging from the continental Afrotropics and Madagascar, throughout South-east Asia to the Pacific and the "Nectar fly" may yet be found occurring naturally outside Australia, or even in Central Africa. Lachaise *et al*. (1988) noted that many species of the *D*. (*S*.) *melanogaster* species-group, to which *D*. *flavohirta* belongs (Bock 1976; Da Lage *et al*. 2007: 57; Grimaldi *et al*. 2015), are poorly known and "… confined to the submontane forest [of the west Cameroon mountains, a poorly surveyed area], characterised by … *Syzygium staudtii* (Engl.) Mildbr." (Lachaise *et al*. 1988: 168).

This species has been recorded to occur super-abundantly in myrtaceous blossom, just meters above a fruit trap on the ground, without a single specimen being lured to the fruit-bait. Most adult specimens collected by the writers have been swept directly from myrtaceous blossom, especially when honeybees were present. Although there is evidence that honeybees avoid infested flowers (Herrmann 1983), leading to a significantly diminished honey yield.

Drosophila (*S*.) *suzukii* (Matsumura, 1931) (Spotted wing *Drosophila*, SWD) is a species of considerable concern for

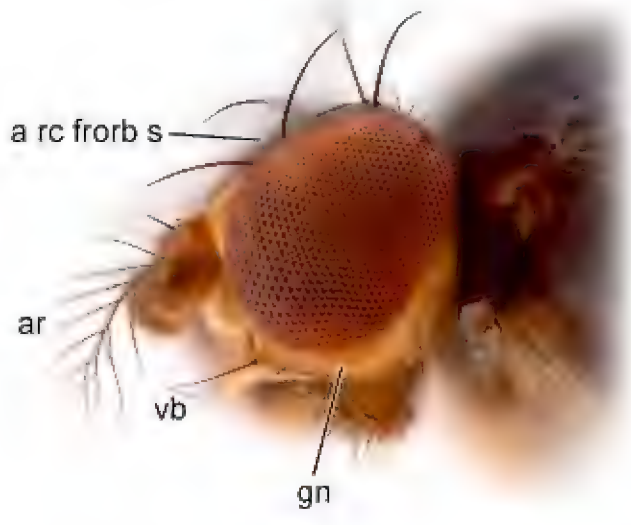


34 *Drosophila* (*Drosophila*)



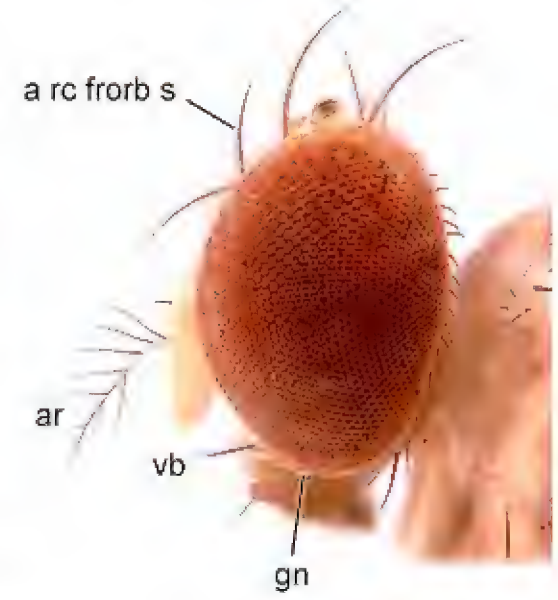
35 *Neotanygastrella*

36 *Cacoxenus* (*Gitonides*)



37 *Liodrosophila*

38 *Gitona*



39 *Leucophenga*

Figs 106.34–39. Heads of Drosophilidae (lateral views): (34) *Drosophila* (*Drosophila*) *punctatonervosa* Frey; (35) *Neotanygastrella* sp.; (36) *Cacoxenus* (*Gitonides*) *notius* Tsacas & Chassagnard; (37) *Liodrosophila divergens* Okada; (38) *Gitona stuckenbergi* Tsacas; (39) *Leucophenga perargentata* Bächli.

Abbreviations: a rc frorb s – anterior reclinate fronto-orbital seta; ar – arista; fc car – facial carina; gn – gena; p rc frorb s – posterior reclinate fronto-orbital seta; pc frorb s – proclinate fronto-orbital seta; prepst s – proepisternal seta; sbvb s – subvibrissal seta; vb – vibrissa.

growers of soft-skinned fruits, such as blueberries, cherries and strawberries. Since 2008, the species has spread rapidly throughout North America (Hauser 2011), western Europe (Calabria *et al*. 2012) and South America (Deprá *et al*. 2014), from China, Japan and Korea. It is of economic importance because, unlike other species in the genus *Drosophila*, it can spoil fruit otherwise suitable for human consumption. Rot spreads from the oviposition puncture hole made in fruit by the female's very large, sclerotised oviscape. High resolution diagnostic images of males and females have been published by McEvey (2017*b*). The species had in late 2013 reached Afrotropical Réunion Is. (V. Balmés, pers. comm. 2013). The globalisation of fruit markets and recent expansion of susceptible fruit production likely resulted in the rapid spread of *D.* (*S.*) *suzukii* and contributed to the rise in its economic impact (Cini *et al*. 2012; Klick *et al*. 2016), as well as the fact that the species breeds well in native berries.

Apart from *Drosophila* (*S.*) *suzukii*, which is of agricultural importance, there are no other representatives of this family that have a direct and negative impact on humans. There are some drosophilids which may have low level significance to human health: *Phortica* Schiner species (six in the Afrotropics), are attracted to lacrymal secretions of humans and some other animals and are known to be intermediate hosts of *Thelazia* species nematodes in Europe (Otranto *et al*. 2012) and Asia (Kamakura *et al*. 1998). Infestation with parasitic *Thelazia* nematodes, or eyeworms, causes injuries with mild to severe symptoms (*e.g*., lacrimation, epiphora, conjunctivitis, keratitis and even corneal ulcers).

The aquatic larvae of *Drosophila* (*D.*) *cogani* Tsacas & Disney, 1974 and *D.* (*D.*) *simulivora*, are predacious on first- and second-instar larvae of *Simulium* species (Simuliidae) (Tsacas & Disney 1974). Simuliid flies in the Afrotropics are associated with river blindness (onchocerciasis).

The larvae of *Gitona ethiopica* Tsacas, 1981 are stemborers of Endod or Gopo berry, *Phytolacca dodecandra* L'Herit. (Phytolaccaceae) in tropical Africa. *Gitona pauliani* Séguy, 1951 may also be a *Phytolacca*-borer in Madagascar (Tsacas & Teshome 1981). The fruit of this plant has a very high molluscicidal property and may be effective in controlling the human disease schistosomiasis. These phytophagous *Gitona* Meigen species may, therefore, impede anti-schistosomiasis programmes in Ethiopia (Tsacas & Teshome 1981) and elsewhere in the Afrotropics.

Classification

Drosophilidae is included within the superfamily Ephydroidea, which also comprises Camillidae, Curtonotidae, Diastatidae (including Campichoetinae) and Ephydridae (Grimaldi 1990*a*; McAlpine 1989: 1486). The large molecular study by Wiegmann *et al*. (2011) proposes a novel addition to this superfamily of the endoparasitoid family Cryptochetidae and the highly specialised family of "Bee louse flies", Braulidae. That study, in fact, hypothesised that Drosophilidae is most closely related to those two small, unusual families.

Drosophilidae is arguably the most intensively studied family of Diptera phylogenetically, certainly based on molecular research, but also with a great deal of morphological study (Fartyal *et al*. 2013; Grimaldi 1990*a*; Hu & Toda 2001, 2002; Okada 1989; Throckmorton 1962, 1966, 1975). Molecular efforts have focused on and around *Drosophila* and, not surprisingly, Drosophilidae was the first family of insects to have multiple genomes fully sequenced (*Drosophila* 12 genomes Consortium 2007). Molecular evidence has exposed some problematic areas of drosophilid classification, although the relationships of genera based on all lines of evidence is slowly converging on a stable consensus. A classification that closely reflects relationships, however, remains taxonomically problematic, as discussed below. The traditional classification of the family into two subfamilies, the Drosophilinae and Steganinae, remains intact, though monophyly of each subfamily has not been rigorously tested molecularly.

In the Drosophilinae, all evidence largely agrees on the early branching positions of *Chymomyza* + *Neotanygastrella* Duda, *Lissocephala* Malloch, *Microdrosophila* and *Scaptodrosophila* within this subfamily (*e.g*., Grimaldi 1990*a*; Hu & Toda 2001; Remsen & O'Grady 2002; Throckmorton 1975). The large genus *Drosophila* is traditionally and currently classified into subgenera and most of these further divided into species-groups (*e.g*., Patterson & Stone 1952: 15; Sturtevant 1942). Subgenera that have been pruned from *Drosophila* and elevated to genera include: *Hirtodrosophila* and *Scaptodrosophila* (Grimaldi 1990*a*), *Dichaetophora* including *Nesiodrosophila* Wheeler & Takada (Hu & Toda 2002) and *Lordiphosa* (Hu & Toda 2001). The subgenus *D.* (*Dorsilopha* Sturtevant) should also be a separate genus. Molecular evidence has confirmed Throckmorton's (1966, 1975) arrangement of *Drosophila sensu stricto* into two main lineages (Morales-Hojas & Vieira 2012; Remsen & O'Grady 2002; Robe *et al*. 2005): the *D. immigrans-tripunctata* "radiation" (defined in part by the presence of a hood-like structure over the distiphallus, articulating with the posterolateral arms of the hypandrium) and the *D. virilis-repleta* "radiation" (in which the cercus is laterally connected to the epandrium). Unfortunately, phylogenetically between these two "radiations" of *Drosophila sensu stricto*, molecular evidence thus far indicates placement of numerous other genera, including the *Liodrosophila* genus-group, *Zaprionus* and two large clades: a mycophagous lineage, consisting of *Hirtodrosophila*, *Mycodrosophila*, *Paramycodrosophila* Duda and *Zygothrica*; as well as *Scaptomyza* (which probably includes the immense radiation of Hawaiian drosophilids). Thus, *Drosophila sensu stricto* appears diphyletic.

Further problematic is the apparently early branching position of the subgenus *D.* (*Sophophora*) among drosophilines, clearly separate from *Drosophila sensu stricto*. The type species of *Drosophila* is *Musca funebris* F., 1787 and the type species of subgenus *D.* (*Sophophora*) is *Drosophila* (*S.*) *melanogaster*, so if drosophilid classification is to closely reflect phylogeny, *D.* (*Sophophora*) should be raised to generic rank. A binomial name change of the most studied eukaryote, to *Sophophora melanogaster*, is highly controversial, as have been alternative suggestions (*e.g*., McEvey *et al*. 2008; O'Grady & Markow 2009; Thompson *et al*. 2008; van der Linde 2007). The problem of the apparent polyphyly of *Drosophila* remains unresolved and should probably await further data on relationships.

Steganinae retain more plesiomorphic features; Drosophilinae are more diverse in species and genera and have attracted

most of the attention by geneticists and evolutionary biologists. The virtually cosmopolitan genus *Leucophenga* is the largest genus of steganines and is very diverse in the Afrotropics. It is closely related to the other large, virtually cosmopolitan genus *Stegana* Meigen and both to the smaller genera *Allopygaea*, *Eostegana* Hendel, *Paraleucophenga*, *Parastegana* Okada and *Pseudostegana* Okada (e.g., Li *et al*. 2013). The *Rhinoleucophenga* genus-group, the larvae of which are predators of Sternorrhyncha (Hemiptera), are mostly New World in distribution. The virtually cosmopolitan *Amiota* genus-group (well-represented in the Afrotropics), comprises *Amiota* Loew *sensu stricto*, *Apenthecia* Tsacas, *Apsiphortica* Okada, *Cacoxenus* Loew, *Gitona*, *Paracacoxenus* Hardy and *Phortica*. The classification of Máca (2003) and Bächli & Vilela (2011) is largely adopted here, in which several former subgenera of *Amiota* and one of *Cacoxenus* were raised to generic rank.

40 *Allopygaea*

41 *Mycodrosophila* (*Mycodrosophila*)

42 *Apenthecia*

43 *Drosophila* (*Drosophila*)

44 *Apenthecia*

45 *Drosophila* (*Sophophora*)

46 *Luzonimyia*

47 *Amiota*

48 *Gitona*

49 *Stegana*

Figs 106.40–49. Antennal aristae of Drosophilidae: (40) *Allopygaea* sp.; (41) *Mycodrosophila* (*Mycodrosophila*) *gratiosa* (de Meijere); (42) *Apenthecia* sp.; (43) *Drosophila* (*Drosophila*) *adamsi* Wheeler; (44) *Apenthecia* sp.; (45) *D.* (*Sophophora*) *flavohirta* Malloch; (46) *Luzonimyia* sp.; (47) *Amiota* sp.; (48) *Gitona stuckenbergi* Tsacas; (49) *Stegana* sp.

Identification

Bächli's (2021) thorough compilation of the taxonomic literature and nomenclatural data for the Drosophilidae is invaluable for many taxonomists, biogeographers, ecologists and evolutionary biologists and remains the most reliable, freely accessible, starting point for most kinds of work on the family. Information on the Afrotropical fauna included in the world catalogue of the Drosophilidae (Brake & Bächli 2008) has changed little since its publication. Papp (2009) described *Hypselothyrea* (*Deplanothyrea*) *zulu* from KwaZulu-Natal, South Africa; *Drosophila* (*S.*) *suzukii* has been reported from the region (see above) and Yassin, with colleagues, have named eight species and synonymised one species of Afrotropical *Zaprionus* (see Bächli 2021).

The below identification key has been constructed based on Bächli (1998), Bock (1982) and Okada (1989). Paired setae and other paired structures are described in the singular, except where the context makes this inappropriate. Drosophilidae are best micro-pinned in the field for later double-mounting (see Chapter 2).

Key to genera of Afrotropical Drosophilidae

1. Thorax with distinct prescutellar setae usually present (e.g., Figs 10, 68); head with anterior reclinate fronto-orbital seta strong (e.g., Figs 32, 39); acrostichal setae in 8 or more rows; antennal arista bare, micro-pubescent or plumose (e.g., Figs 40, 42, 44, 46–49); mid and hind tarsi with seriate seam setulae; male terminalia with surstylus often without prensisetae; female oviscapt commonly without tooth-like pegs (STEGANINAE) 2

– Thorax with prescutellar setae usually absent (e.g., Fig 19), if present (some *Scaptodrosophila*), then anterior reclinate seta small; acrostichal setae in 8 or fewer rows (e.g., Fig. 19); antennal arista plumose, with at least 1 ventral branch (e.g., Figs 41, 43, 45); mid and hind tarsi usually without seriate seam setulae; male terminalia with surstylus usually with prensisetae (e.g., Fig. 75); female oviscapt commonly with tooth-like pegs (DROSOPHILINAE) 12

2. Antennal arista entirely bare (e.g., Fig. 42) or micro-pubescent (e.g., Figs 44, 46, 48) 3

– Antennal arista plumose, with long (e.g., Figs 40, 41, 47) or short, straight branches (e.g., Figs 45, 49) . . . 6

3. Head with posterior reclinate fronto-orbital seta either scale-like (Fig. 69), or as short as, or shorter than, anterior reclinate fronto-orbital seta and distinctly thickened (Fig. 33) . . . . . *Apenthecia* Tsacas

– Head with posterior reclinate fronto-orbital seta long, as long, or longer than, proclinate fronto-orbital seta, not scale-like and not short and unusually thickened (e.g., Figs 20, 35) 4

4. Thorax with strong greyish pruinescence (Figs 15, 68) . . . . . *Luzonimyia* Malloch

– Thorax without strong greyish pruinescence (e.g., Figs 3, 5, 9) 5

5. Head with facial carina rudimentary (Fig. 36); thorax with acrostichal setae in 10 rows; wing crossvein *bm–m* strong; basal medial (*bm*) and discal medial (*dm*) cells separate; costal vein (*C*) strong beyond vein R_{4+5}, reaching vein M_1; wing clear . . . . . *Cacoxenus* Loew

– Head with facial carina prominent (Fig. 38); thorax with acrostichal setae in 8 rows; wing crossvein *bm–m* absent or weak; basal medial (*bm*) and discal medial (*dm*) cells confluent, or virtually so (Fig. 53); costal vein (C) weak beyond vein R_{4+5}; wing often with dark maculae at tips of veins R_{2+3} and R_{4+5} (Fig. 53) . . . . . *Gitona* Meigen

6. Antennal arista with short branches; if branches long, then these straight (e.g., Fig. 47) 7

– Antennal arista with long curved branches above and long (e.g., Fig. 41) or short (e.g., Fig. 40) branches below 9

7. Thorax with milky white macula on postpronotum and below wing base (Figs 16, 25) . . . *Amiota* Loew

– Thorax without milky white macula on postpronotum and below wing base 8

8. Thorax with anepisternum setose . . . . . *Apsiphortica* Okada

– Thorax with anepisternum bare . . . . . *Phortica* Schiner

9. Antennal arista with long branches above and short branches below (e.g., Fig. 40); third costal sector without short peg-like setae ventrally (e.g., Fig. 13) 10

– Antennal arista plumose with long branches above and below (e.g., Figs 39, 49); third costal sector with short peg-like setae ventrally (e.g., Figs 51, 67) 11

10. Scutellum without supernumerary setae; male abdominal tergites not pruinescent (Fig. 13); male terminalia without surstylus . . . . . *Allopygaea* Tsacas

– Scutellum with supernumerary setae; male abdominal tergites pruinescent; male terminalia with well-developed surstylus . . . . . *Paraleucophenga* Hendel

11. Wing with discal medial (*dm*) and basal medial (*bm*) cells confluent (Figs 10, 11, 52) . . . . *Leucophenga* Mik
– Wing with discal medial (*dm*) and basal medial (*bm*) cells separate (Fig. 51) . . . . . *Stegana* Meigen
12. Costal wing vein (C) extended at distal incision, forming blackened lappet (e.g., Figs 14, 17, 18, 50, 55) 13
– Costal wing vein (C) not extended at distal incision, not forming blackened lappet (e.g., Figs 54, 56–63) 14
13. Thorax with mesoscutum patterned (Figs 14, 18), with 2 pairs of dorsocentral setae . . . . . *Dettopsomyia* Lamb
– Thorax with mesoscutum not patterned (Fig. 17), with 1 pair of dorsocentral setae . . . . . *Mycodrosophila* (*Mycodrosophila* Oldenberg)
14. Thorax with anterior dorsocentral seta large, inserted near transverse suture (Fig. 12); wing tip somewhat pointed (Fig. 12); subcostal break deep, but not blackened; head with frons much broader than long . . . . . *Microdrosophila* Malloch
– Thorax with anterior dorsocentral seta smaller than posterior dorsocentral seta, not inserted close to transverse suture (e.g., Fig. 19), or absent (e.g., Fig. 17); subcostal break shallow, or if deep, then associated with blackened costal lappet; head with frons squarish, tapered or longer than broad (e.g., Figs 1, 19, 64) 15
15. Scutellum distinctly upturned or head without postocellar setae; thorax with 1 katepisternal seta . . . . . *Hypselothyrea* de Meijere
– Scutellum not upturned; head with postocellar setae; thorax with at least 2 large katepisternal setae 16
16. Head with frons highly polished (e.g., Fig. 65), or wing with dark markings along costal margin (e.g., Figs 59–61) and anterior edge of frons, overhanging antennal bases (e.g., Fig. 64) 17
– Head with frons not highly polished (e.g., Figs 19, 71–73); wing either hyaline and unpatterned (e.g., Fig. 54) or patterned, but not as described above (e.g., Figs 56–58, 62, 63) 18
17. Head with frons highly polished, clearly incised by dull line or band on each side (Fig. 65), anterior edge not protruding over antennal bases (Fig. 65) . . . . . *Liodrosophila* Duda
– Head with frons not polished, without dull lines or bands (Fig. 64), anterior edge protruding over antennal bases (Fig. 64) . . . . . *Lissocephala* Malloch
18. Thorax with mesoscutum with longitudinal silvery-white stripes (e.g., Figs 6, 7, 22, 71–73) 19
– Thorax with mesoscutum without longitudinal silvery-white stripes (e.g., Fig. 19) 21
19. Thorax with 3 pairs of dorsocentral setae; prescutellar acrostichal setae well-developed . . . . . *Zaropunis* Tsacas
– Thorax with 2 pairs of dorsocentral setae; prescutellar acrostichal setae undifferentiated or only slightly enlarged 20
20. Head with posterior reclinate fronto-orbital seta fine, inserted closer to proclinate seta, orbito-index *ca* 0.6; male terminalia with epandrium truncate below; hypandrium with 2–3 long submedial setae . . . . . *Phorticella* Duda
– Head with posterior reclinate fronto-orbital seta strong, closer to inner vertical than to proclinate seta (Fig. 22), orbito-index > 1.0 (Fig. 22); male terminalia with epandrium pointed below; hypandrium with short submedial setae . . . . . *Zaprionus* Coquillett
21. Head with anterior reclinate fronto-orbital seta large, subequal to proclinate fronto-orbital seta, inserted well anterior to it (Fig. 23); postocellar setae minute; face short and flat (Fig. 23) . . . . . *Chymomyza* Czerny
– Head with anterior reclinate fronto-orbital seta not subequal to proclinate fronto-orbital seta, usually small or minute, inserted, at most, only slightly before proclinate fronto-orbital seta (e.g., Figs 24, 26, 31, 34, 35); face carinate or convex, seldom short and flat. 22
22. Thorax with mesoscutum with 1 pair of dorsocentral setae (anterior dorsocentral seta absent) (Fig. 17); scutellum rounded (Fig. 9), velvety; mesoscutum subshiny black or very dark brown and pleura often whitish (Figs 9, 17); wing with apex of costal vein (C) at distal costal incision (subcostal break) if darkened, then not protruding as blackened lappet . . . . . *Mycodrosophila* (*Promycodrosophila* Okada)
– Thorax with mesoscutum with 2 or more pairs of dorsocentral setae (e.g., Figs 6, 8, 19); scutellum triangulate or tapered apically (e.g., Fig. 19); mesoscutum black, grey, or brown, patterned or plain, and

if thorax black above and white laterally, then 2 or more pairs of dorsocentral setae present; wing with apex of costal vein (*C*) at distal costal incision not expanded into blackened lappet 23

23. Head with facial carina low or obsolete between antennae, protuberant below at level of vibrissa (e.g., Grimaldi 1990*a*, fig. 279) (Fig. 35) . . . . . *Neotanygastrella* Duda

– Head with facial carina nose-like, ridged, bulbous, or absent and not as above (e.g., Figs 22, 34) . . . 24

24. Head with ocellar setae positioned outside ocellar triangle, inserted lateral to, or forward of, median ocellus (e.g., Fig. 26) 25

– Head with ocellar setae positioned inside ocellar triangle (e.g., Figs 19, 64, 65, 71) 26

25. Wing vein R_{2+3} straight (e.g., Lamb 1914, fig. 21), or only slightly curved (e.g., Burla 1954, fig. 123), where it meets costal vein (*C*). . . . . *Dichaetophora* Duda

– Wing vein R_{2+3} turned abruptly costad (Figs 56–58) . . . . . *Jeannelopsis* Séguy

26. Proboscis exceptionally long, projected anteriad (e.g., Grimaldi 1990*b*, figs 4, 5) . . . . . *Zygothrica* Wiedemann

– Proboscis not exceptionally long, usually withdrawn 27

27. Thorax with 3 large subequal katepisternal setae; head with single vibrissa; thorax with prescutellar acrostichal setae usually enlarged; proepisternal seta small or minute (as in *Chymomyza bicolor* Lamb, 1914, Fig. 23) sometimes present; antennal postpedicel without long setulae . . . . . *Scaptodrosophila* Duda

– Thorax with 1 or 2 large katepisternal setae, if 3, then unequal in length; head with single vibrissa or subvibrissae not more than ½ vibrissa length; prescutellar setae barely or not enlarged; proepisternal seta absent; antennal postpedicel with long setulae in some species. 28

28. Head with single vibrissa; antennal postpedicel often elongate, or with exceptionally long setulae (as in *Leucophenga paracapillata* Bächli, 1971, Fig. 21); males never with sex combs; head not gradually rounded posterior to level of ocellar triangle (*i*.e., vertex not rounded in lateral view). . . . . *Hirtodrosophila* Duda

– Head with subvibrissal or oral setae either large and subequal to vibrissa (e.g., Fig. 34) or smaller; antennal postpedicel never with setulae as long as width of postpedicel; head with vertex either rounded or square-shaped (in lateral view) (e.g., Figs 20, 34) 29

29. Head with vertex not distinctly rounded (in lateral view) (Fig. 20); thorax with acrostichal setae in 4, 6 or 8 rows between dorsocentral setae (Fig. 19). . . . . *Drosophila* Fallén

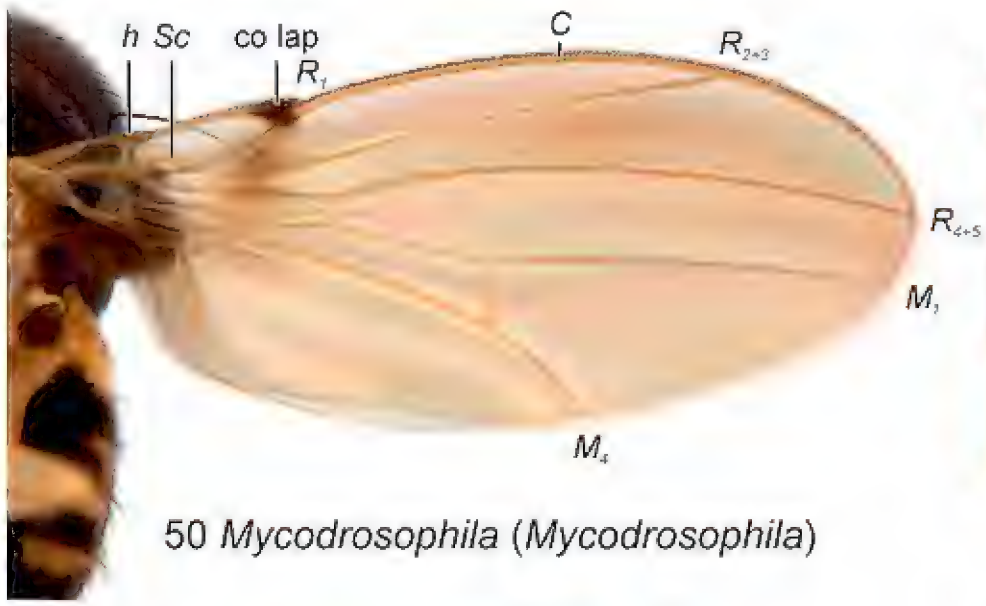
– Head with vertex rounded (in lateral view); thorax with acrostichal setae usually in 2 rows between dorsocentral setae . . . . . *Scaptomyza* Hardy

Synopsis of the fauna

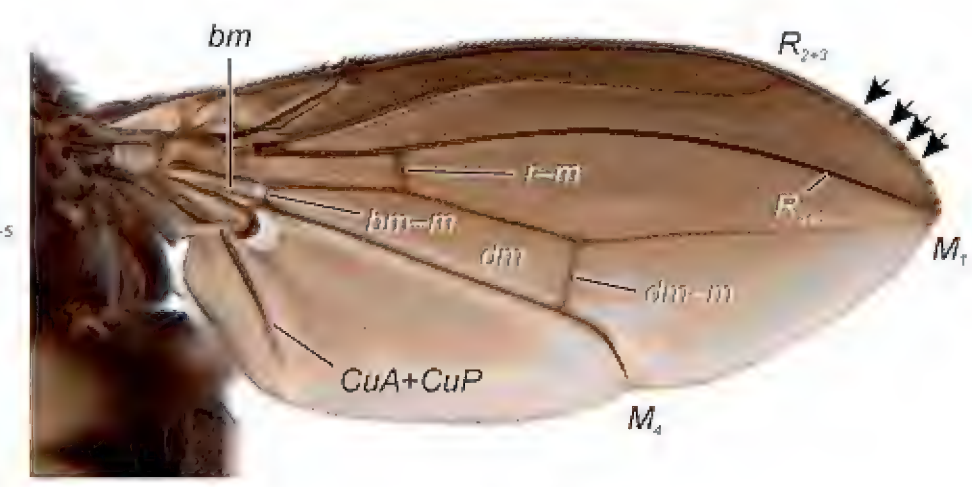
Globally, there are currently 4,369 described extant species of Drosophilidae in 77 genera and three genera are known only from amber. Among acalyptrate families it is second in species diversity only to the Tephritidae and may eventually be found to be larger. Of the 74 extant genera, 45 are classified in the subfamily Drosophilinae and 28 in Steganinae, while *Sphyrnoceps* de Meijere remain *incertae sedis*. The drosophilid fauna of the Afrotropical Region comprises *ca* 479 described species in 29 genera. In 1981, there were 291 described species in 18 genera (plus 63 known, but undescribed) and it was estimated then that the number could be as high as 500 (Tsacas *et al*. 1981: 201), it is very likely to climb to 1,000 species, if more extensive fieldwork can be undertaken in Central Africa, the Eastern Arc Mountains of Kenya and Tanzania and Madagascar before loss of habitat. By comparison, the Australasian Region (including the very diverse New Guinea fauna and the Hawaiian radiation of *Idiomyia* Grimshaw and *Scaptomyza* species), has *ca* 1,150 described species in 47 genera. The Oriental Region has more than 1,300 described species in 40 genera and the Neotropical Region has *ca* 1,000 species in 34 genera, with many more species awaiting description.

In terms of number of species, the largest genera in the Afrotropical Region are *Drosophila*, with over 159 species (90 in the subgenus *D*. (*Sophophora*), 64 in *Drosophila sensu stricto*), *Leucophenga* with 69 species and *Zaprionus* with 47 species. Many undescribed species of *Hirtodrosophila*, *Microdrosophila*, *Mycodrosophila* and *Scaptodrosophila* are known.

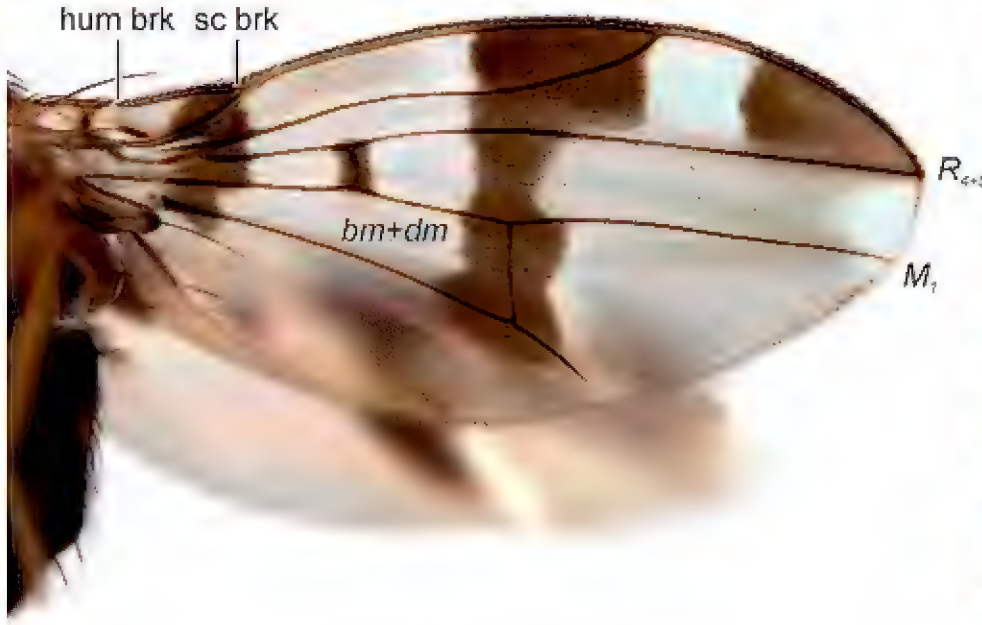
Two genera are endemic to the region: *Allopygaea* (morphologically close to *Paraleucophenga* with three species) and *Zaropunis* Tsacas (monotypic, South Africa). *Jeannelopsis* should no longer be treated as endemic (see below). Biogeographically, Madagascar and to a lesser extent, the Mascarene Is., have a rich endemic and diverse fauna that still requires much work taxonomically. Since the small fauna (36 species) of Seychelles was described very early (Lamb 1914), several widespread Afrotropical and some global species, have Seychelles as the type locality. *Chymomyza bicolor*, *Dettopsomyia formosa* Lamb, 1914 and *Drosophila* (*D*.) *nasuta* have ranges beyond the Afrotropical Region. *Dichaetophora aberrans* (Lamb, 1914), *Drosophila hirtipes* Lamb, 1914, *Mycodrosophila* (*M*.) *fracticosta* (Lamb, 1914), *M*. (*M*.) *nigerrima* (Lamb, 1914), *Scaptodrosophila finitima* (Lamb, 1914), *S. rufuloventer* (Lamb, 1914) and *S. triangulifer* (Lamb, 1914), are thought to



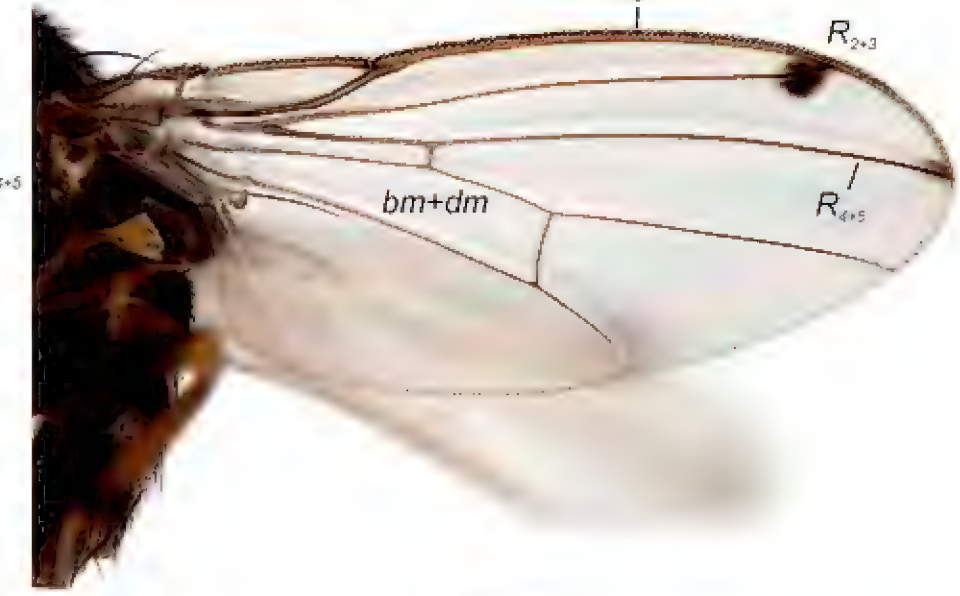
50 *Mycodrosophila* (*Mycodrosophila*)



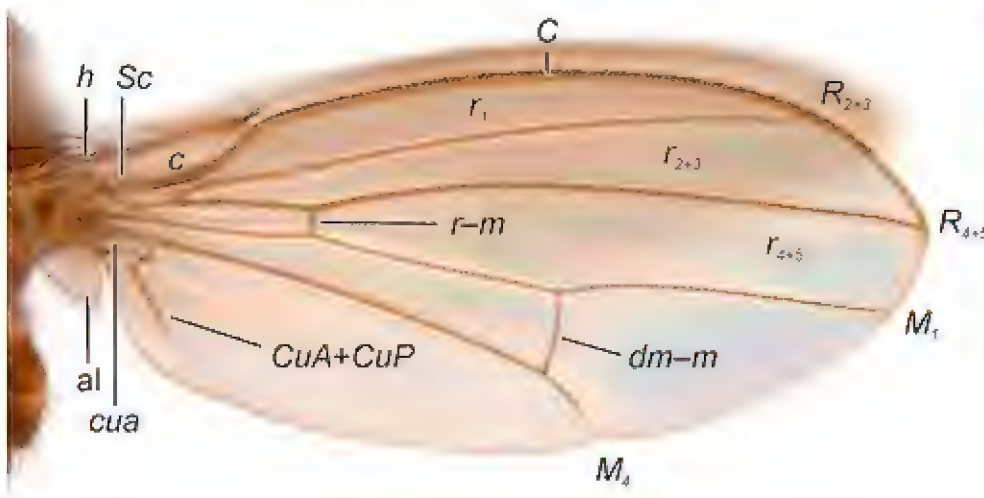
51 *Stegana*



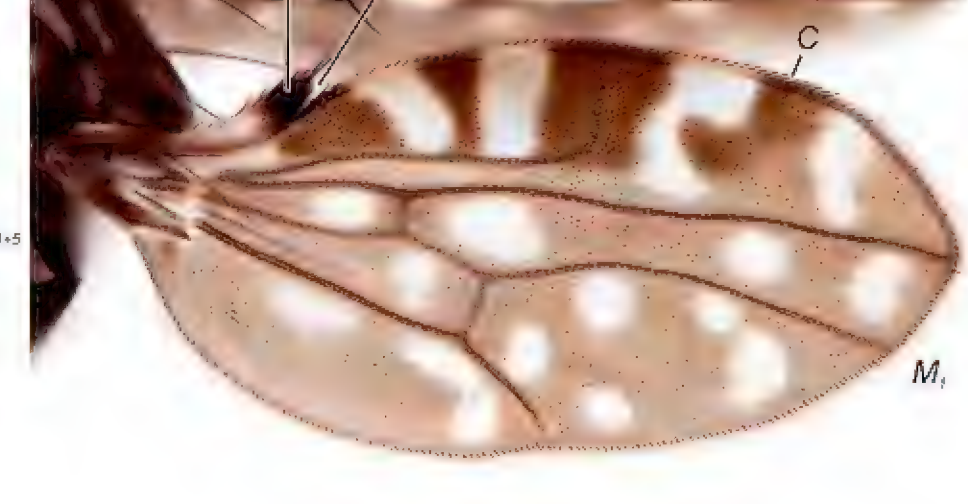
52 *Leucophenga*



53 *Gitona*



54 *Drosophila* (*Drosophila*)



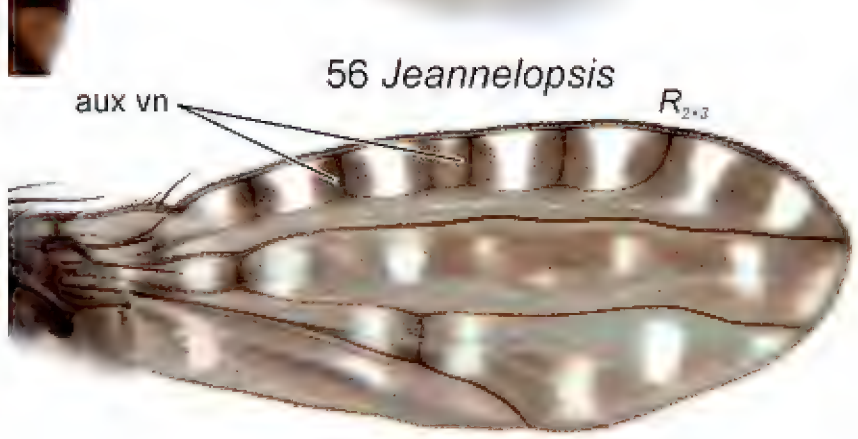
55 *Dettopsomyia*

Figs 106.50–55. Wings of Drosophilidae (dorsal views): (50) *Mycodrosophila* (*Mycodrosophila*) *fracticosta* (Lamb); (51) *Stegana* sp.; (52) *Leucophenga cuthbertsoni* Malloch; (53) *Gitona stuckenbergi* Tsacas; (54) *Drosophila* (*Drosophila*) *funebris* (F.); (55) *Dettopsomyia formosa* Lamb.

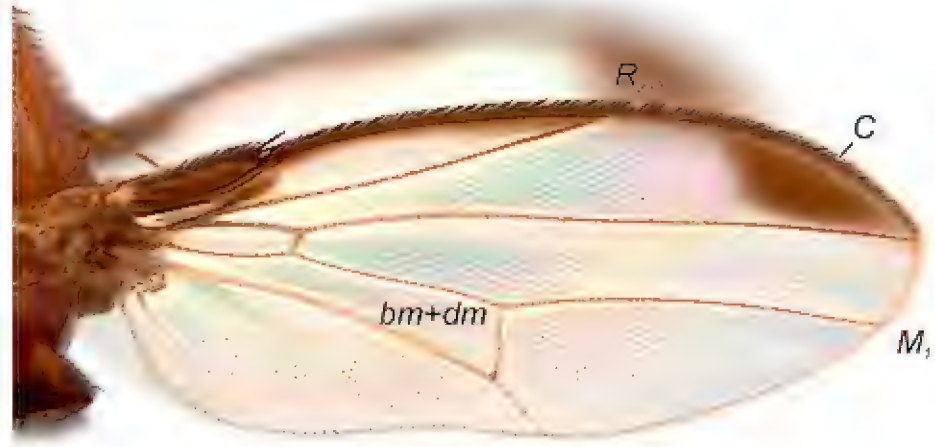
Abbreviations: al – alula; *bm* – basal medial cell; *bm+dm* – basal medial cell + discal medial cell; *bm–m* – basal medial crossvein; *c* – costal cell; *C* – costal vein; co lap – costal lappet; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *dm* – discal medial cell; *dm–m* – discal medial crossvein; *h* – humeral crossvein; hum brk – humeral break; M_1 – first branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; r_1 – first radial cell; R_{2+3} – second branch of radius; r_{2+3} – second radial cell; R_{4+5} – third branch of radius; r_{4+5} – third radial cell; *r–m* – radial–medial crossvein; *Sc* – subcostal vein; sc brk – subcostal break.

56 *Jeannelopsis*

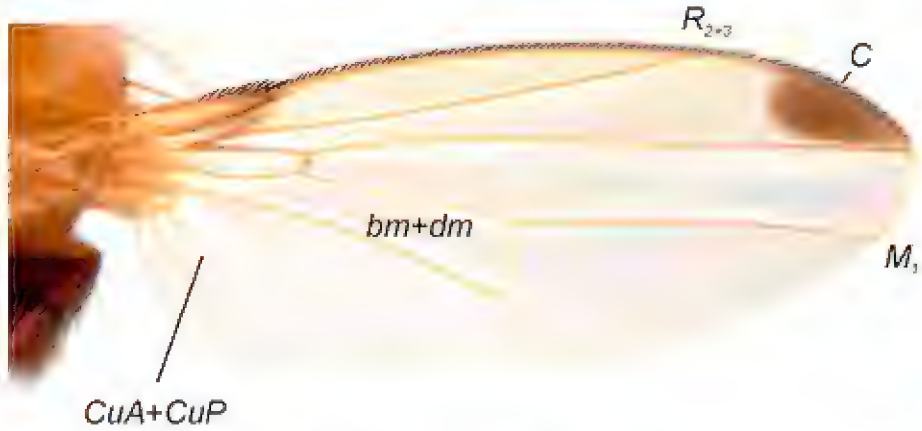
57 *Jeannelopsis*



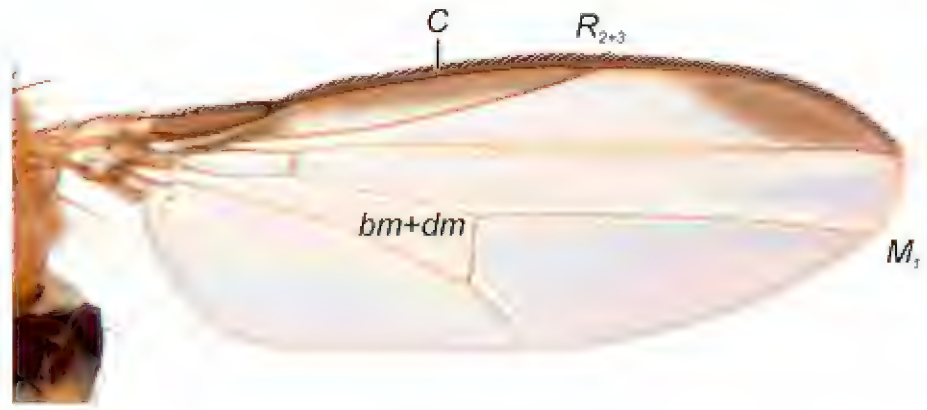
58 *Jeannelopsis*



59 *Lissocephala*

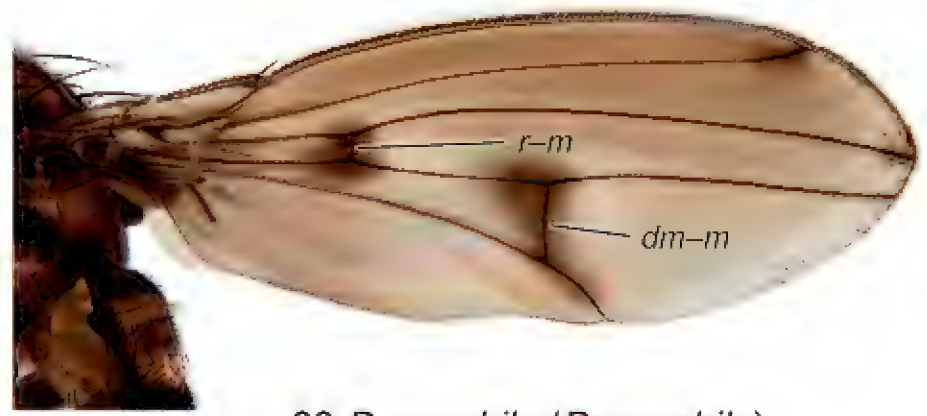


60 *Lissocephala*



61 *Lissocephala*

62 *Drosophila* (*Drosophila*)



63 *Drosophila* (*Drosophila*)

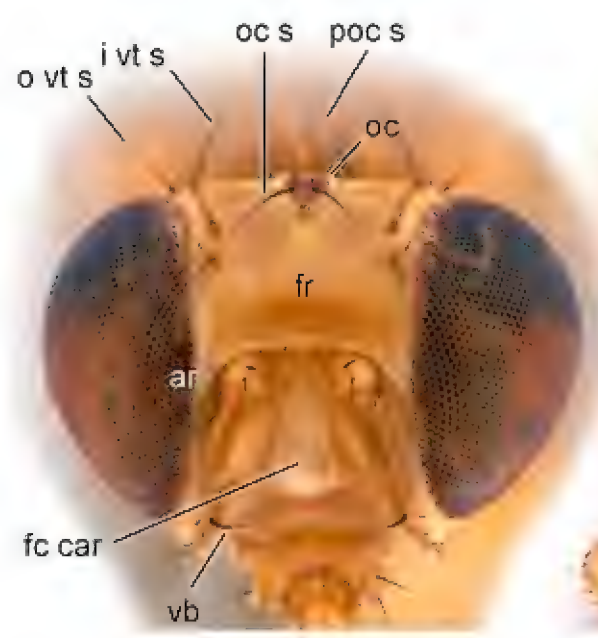
Figs 106.56–63. Wings of Drosophilidae (dorsal views): (56) *Jeannelopsis aneura* Tsacas; (57) *J. zophoptera* Tsacas; (58) *J. mirabilis* Séguy; (59) *Lissocephala disjuncta* Tsacas & Chassagnard; (60) *L. bergi* Chassagnard & Tsacas; (61) *L. ambigua* Tsacas & Chassagnard; (62) *Drosophila* (*Drosophila*) *punctatonervosa* Frey; (63) *D.* (*D.*) *adamsi* Wheeler.

Abbreviations: aux vn – auxiliary veins; *bm+dm* – basal medial cell + discal medial cell; *C* – costal vein; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *dm–m* – discal medial crossvein; M_1 – first branch of media; R_{2+3} – second branch of radius; *r–m* – radial–medial crossvein.

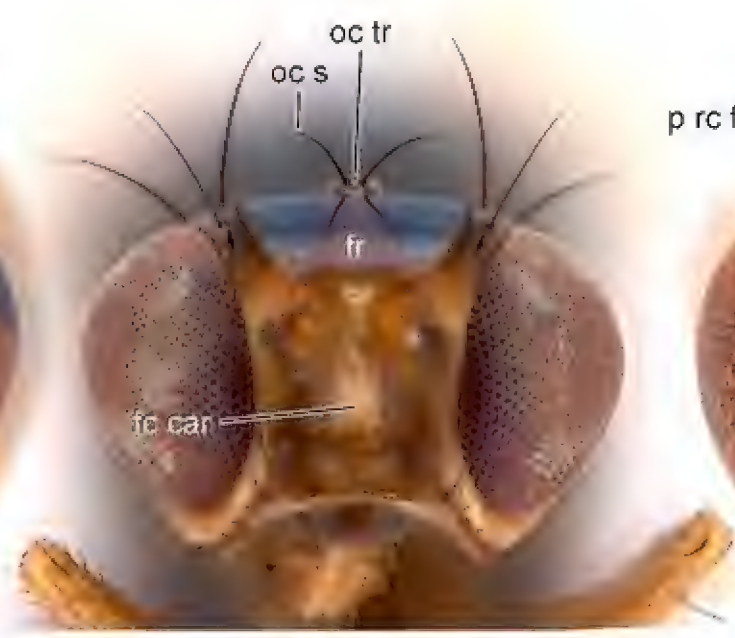
occur in other parts of the Afrotropical Region (Cariou *et al*. 2009, table 2). Definitive comparative studies of topotypic Seychellian flies and extralimital specimens are lacking or unreported. This early taxonomic history, together with the geographical proximity of Seychelles to Madagascar, makes familiarity with the Seychelles drosophilid fauna a necessary first step in any taxonomic study of the Malagasy fauna and indeed of the Afrotropical fauna as a whole. The reduced wings of drosophilids endemic to the remote southern Atlantic islands of Tristan da Cunha are enigmatic and warrant further study (Frey 1954: 16–34; Hackman 1959).

Tsacas *et al*. (1981: 211) estimated that the drosophilid fauna of the Afrotropical Region is 91% endemic, but since the widespread species are well-known and as the number of invasive species is not likely to climb at a rate higher than the rate of discovery of localised species, the percentage endemicity is likely to rise. Conversely, climate change and habitat loss may result in high rates of extinction and increased vulnerability to invasive species, these trends would reduce the percentage endemicity. The introduction and dramatic increase in abundance of *Drosophila* (*Sophophora*) *malerkotliana* Parshad & Paika, 1965 and to a lesser extent *D*. (*D*.) *nasuta*, in Seychelles during the past 100 years may have replaced local endemics. Cariou *et al*. (2009: 380, table 2) showed that intensive fieldwork from 1986–2009 failed to re-discover 12 species (29% of the fauna), that were present or common during surveys of the period 1908–1909 and 1977–1985, but all 22 species present in 1908–1909 were re-collected in 1977–1985. Habitat degradation and loss during the past 40 years is the most likely cause of diminished species diversity.

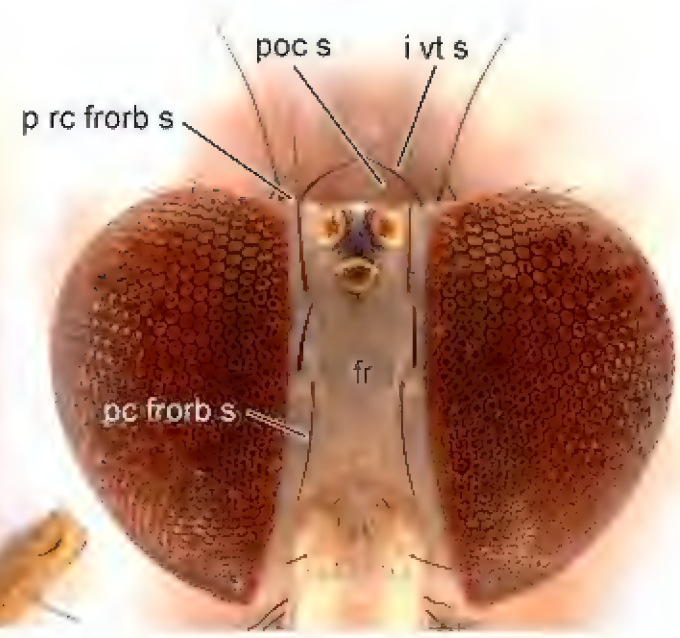
***Allopygaea* Tsacas** (Steganinae)**.** An endemic genus of three described species: *A. bicolor* Tsacas, 2000, described from



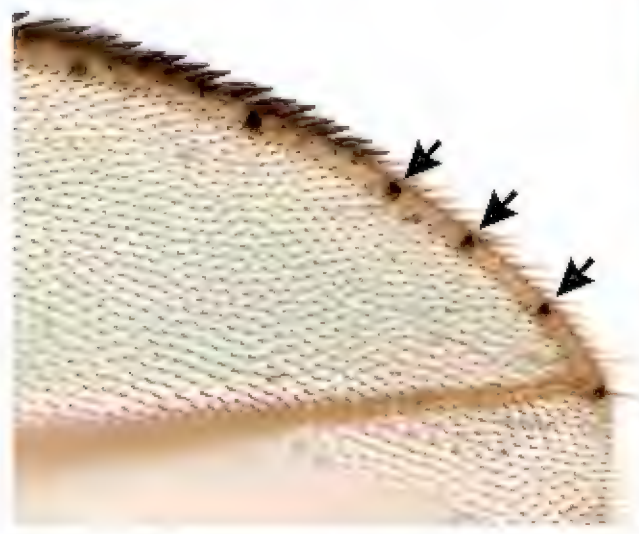
64 *Lissocephala*



65 *Liodrosophila*

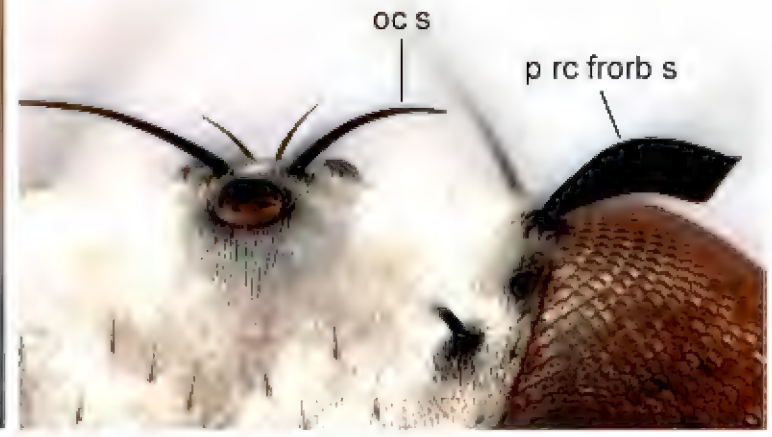


66 *Leucophenga*



67 *Leucophenga*

68 *Luzonimyia*



69 *Apenthecia*

Figs 106.64–69. Head, wing and scutellar features of Drosophilidae: (64) head of *Lissocephala disjuncta* Tsacas & Chassagnard, frontal view; (65) same, *Liodrosophila divergens* Okada; (66) same, *Leucophenga perargentata* Bächli; (67) apical section of wing of *Le. perargentata*, ventral view (costal pegs arrowed); (68) posterior part of scutum of *Luzonimyia* sp., dorsal view; (69) vertex of head of *Apenthecia* sp., frontal view showing scaleiform posterior reclinate fronto-orbital seta.

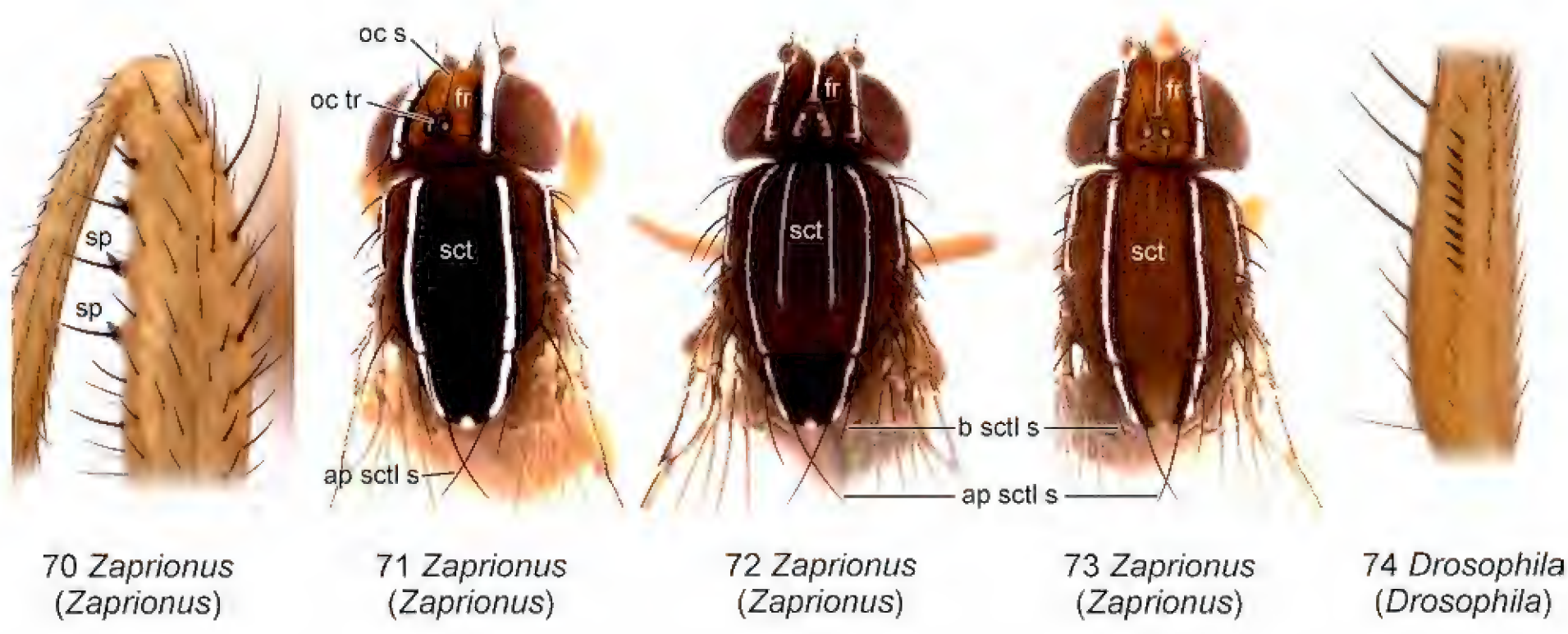
Abbreviations: ar – arista; fc car – facial carina; fr – frons; i vt s – inner vertical seta; o vt s – outer vertical seta; oc – ocellus; oc s – ocellar seta; oc tr – ocellar triangle; p rc frorb s – posterior reclinate fronto-orbital seta; pc frorb s – proclinate fronto-orbital seta; poc s – postocellar setae; pre sctl s – prescutellar setae; sctl – scutellum; vb – vibrissa.

Benin; *A. inexpectata* Tsacas, 2000, from Côte d'Ivoire and Nigeria; and *A. microphalla* Tsacas, 2000, from Benin. Tsacas (2000) included an additional unnamed species from Democratic Republic of Congo and an undescribed species is known from Madagascar (Fig. 13). The genus is closely related to *Paraleucophenga*, but is distinguished by the scutellum with only four setae (more in *Paraleucophenga*) and the male terminalia without a surstylus. Other distinguishing features include a flat face (no carina), the costal wing vein (C) without thorn-like spinules and the antennal arista (Fig. 40), with only the dorsal branches well-developed (Tsacas 2000). The biology and immature stages remain unknown. An identification key to the three species was provided by Tsacas (2000).

***Amiota* Loew** (Steganinae)**.** *Amiota sensu stricto* comprises *ca* 133 species, occurring in all zoogeographical regions, except Antarctica. Three species occur in the Afrotropics: *A. bandai* Chassagnard & Tsacas, 1997, described from Malawi; *A. melanoleuca* Tsacas, 1990, from Botswana and *A. perpusilla* (Walker, 1849), from Sierra Leone. About five other undescribed species are known from Central and Southern Africa and islands of the Indian Ocean. The genus is currently recognised in a much more restricted sense, as just the species traditionally placed in the subgenus *A.* (*Amiota*); the species formerly placed in *Apsiphortica*, *Phortica* and *Sinophthalmus* Coquillett are now in subgenera of *Phortica sensu lato* (Brake & Bächli 2008: 282; Máca 2003). As with most species, Afrotropical species are black with a contrasting white or light postpronotum (Figs 16, 25); the face is flat with a white oral margin and the antennal arista is short-plumose (Fig. 47). Males have complex terminalia, with the hypandrium narrow and U-shaped, the surstylus with a comb-like row of prensisetae, the phallus small and vestigial and the phallapodeme large and plate-like. Males swarm around the heads of humans and other large animals, presumably attracted to perspiration and eye secretion, much like the related genus *Phortica*. Where known from other parts of the world, the larvae of *Amiota* species develop in injured or decaying wood of standing trees. Biology and immature stages otherwise remain unknown. An identification key to Afrotropical species was provided by Chassagnard *et al*. (1997).

***Apenthecia* Tsacas** (Steganinae)**.** A genus of 15 species, occurring in the Afrotropical, Oriental and Palaearctic Regions. The genus is divided into two subgenera: *A.* (*Parapenthecia* Toda & Peng), with five species in China, Indonesia and Palau; and *Apenthecia sensu stricto* with ten species that are endemic to the Afrotropics, principally distributed in East and Southern Africa. No additional undescribed species are known. *Apenthecia* are brown to greyish, pruinescent flies (sometimes with a fasciate scutum), the antennal arista is bare or pubescent (Fig. 44), the facial carina is low and rounded and the posterior reclinate fronto-orbital seta is short and thick (Fig. 33), or in the form of a scale (Fig. 69). The extent of darkening of the distal and proximal annuli of the hind tibiae provides a useful diagnostic (McEvey *et al*. 1988). The Afrotropical species appear to be strictly associated with flowers of endemic *Aloe* (Liliaceae) and possibly the related genus *Kniphofia* (Chassagnard *et al*. 1997; Tsacas 1983). Biology and immature stages otherwise remain unknown. An identification key to Afrotropical species was provided by Chassagnard *et al*. (1997).

***Apsiphortica* Okada** (Steganinae)**.** A genus of eight described species, six from China, *A. lini* (Okada, 1971) from Taiwan in the Palaearctic and the Afrotropical *A. holubi* Máca, 2003, from Zimbabwe (Máca 2003). Distinguishing features of the genus include a setose anepisternum, fusion of the phallus and phallapodeme, the plate-like hypandrium, the surstylus without prensisetae, the antennal arista short-plumose and the facial carina present. Males, like those of *Amiota sensu stricto* and *Phortica sensu lato*, are attracted to lachrymal secretions,



70 *Zaprionus* (*Zaprionus*) | 71 *Zaprionus* (*Zaprionus*) | 72 *Zaprionus* (*Zaprionus*) | 73 *Zaprionus* (*Zaprionus*) | 74 *Drosophila* (*Drosophila*)

Figs 106.70–74. Heads, thoraces and leg features of Drosophilidae: (70) fore femur of *Zaprionus* (*Z.*) *vittiger* Coquillett, posterior view; (71) head and thorax of *Z.* (*Z.*) *ghesquierei* Collart, dorsal view; (72) same, *Z.* (*Z.*) *sexvittatus* Collart; (73) same, *Z.* (*Z.*) *tuberculatus* Malloch; (74) fore femur of *Drosophila* (*Drosophila*) *nasuta* Lamb, posteroventral view.

Abbreviations: ap sctl s – apical scutellar seta; b sctl s – basal scutellar seta; fr – frons; oc s – ocellar seta; oc tr – ocellar triangle; sct – scutum; sp – spine.

especially around human eyes (Cao *et al*. 2007). Biology and immature stages otherwise remain unknown. An identification key to six species, including the Afrotropical species, was provided by Cao *et al*. (2007) and a key to all species from China by Gong & Chen (2018).

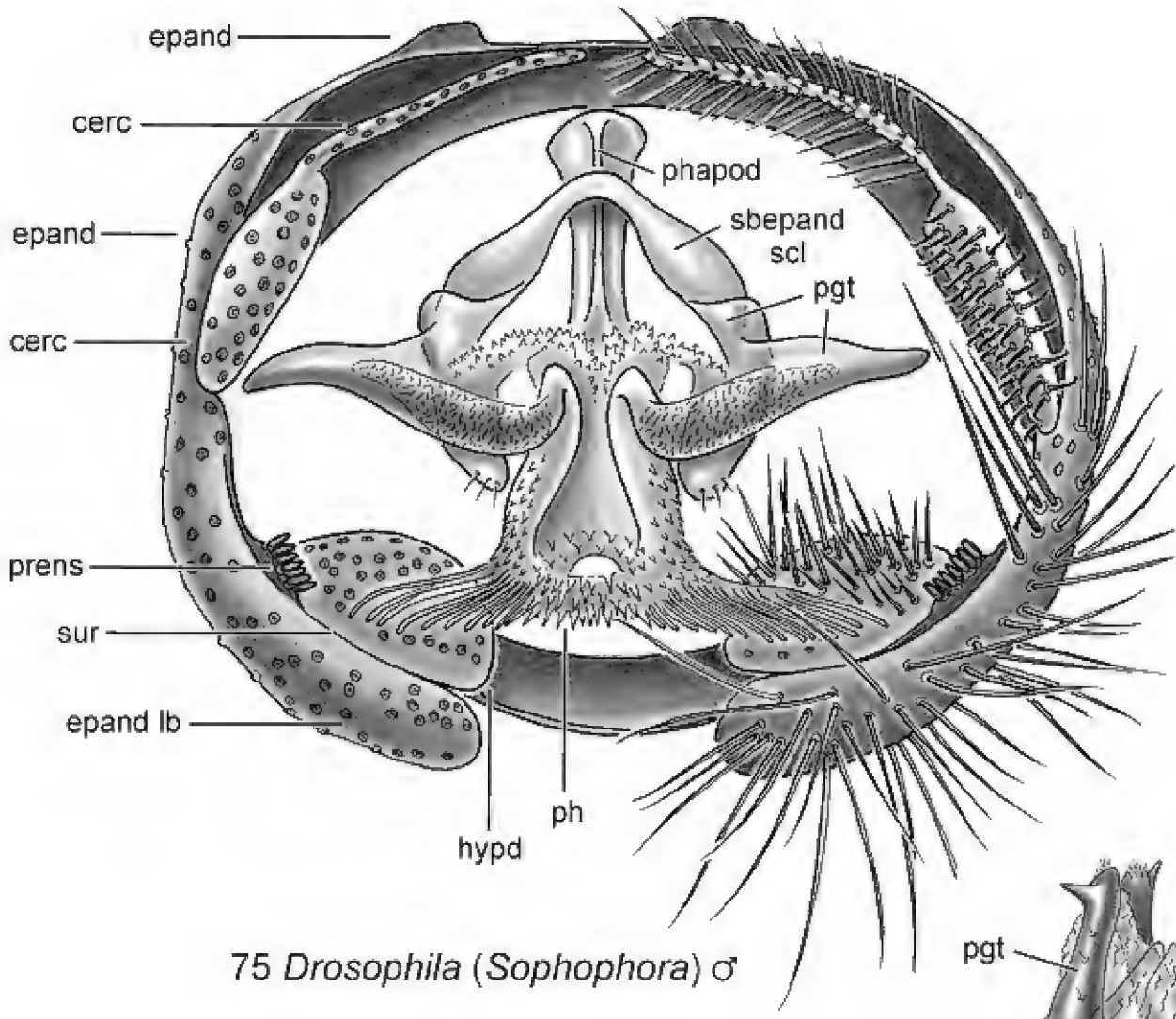
***Cacoxenus* Loew** (Steganinae)**.** A virtually cosmopolitan genus of 33 species, occurring in all zoogeographical regions, except the Neotropical Region and Antarctica. The genus is currently divided into five subgenera (Brake & Bächli 2008: 258), one species from Russia is *incertae sedis*: *Cacoxenus sensu stricto* (one species, Eurasia); *Ca*. (*Nankangomyia* Máca & Lin) (six species, China and South-east Asia); *Ca*. (*Phragmitoxenus* Gornostayev) (one species, central Asia); and *Ca*. (*Gitonides* Knab) (24 species: 12 Afrotropical; two Australasian, 10 Oriental; three Palaearctic, with some overlap) (Fig. 36). The Afrotropical species are distributed mostly in Central and East Africa with one species each in South Africa and Réunion Is. No additional undescribed species are known. Males of *Cacoxenus* are distinguished by the array of large, tooth-like prensisetae on the surstylus of the terminalia. The Eurasian species *Ca*. (*Ca*.) *indagator* Loew, 1858 is a commensal/kleptoparasite in the nests of *Megachile* (*Chalicodoma* Lepeletier) (Hymenoptera: Megachilidae) solitary bees; a biology like that of the Central and West African species *Ca*. (*Gitonides*) *apidoxenus* Tsacas & Desmier de Chenon, 1976 (Ashburner 1981: 400). Many other species of *Ca*. (*Gitonides*) are larval predators of scale insects (Tsacas & Chassagnard 1999). An identification key including the Afrotropical species was provided by Tsacas & Chassagnard (1999).

***Chymomyza* Czerny** (Drosophilinae)**.** A genus of 55 described species, occurring in all zoogeographical regions, except Antarctica, six of which have been described from the Afrotropical Region, reported from Côte d'Ivoire (four species), Seychelles and South Africa. One of these, *Ch. bicolor*, very closely resembles the widespread species *Ch. procnemis* (Williston, 1896) and is a probable synonym with it (Cariou *et al*. 2009: 362), requiring direct comparison of types. Two possibly undescribed species are known from Republic of Congo and Swaziland. The most distinguishing feature of *Chymomyza* species is the size and position of the anterior reclinate fronto-orbital seta (Fig. 23) which, unlike other drosophilines, is large and inserted far forward. *Chymomyza yvettae* Tsacas, 1990 has males with an expanded head and lacks a milky-white macula at the wing tip, characteristic of the *Ch. aldrichii* species-group, while all other Afrotropical species are ascribed to the *Ch. procnemis* species-group, having a milky white macula apically in the wing. Otherwise, the genus is distinguished by the anterior reclinate fronto-orbital seta large and inserted well anterior to the proclinate fronto-orbital seta, close to the anterior frontal margin (Fig. 23); the antennal arista is plumose; the ocellar setae are present, the postocellar setae are small; the vibrissa is present, with other oral setae large; the upper parts of the compound eye is bare, the lower front part has a few enlarged ommatidia; the facial carina is at most small and confined to upper part of the face (Fig. 23); two dorsocentral setae are present; a fine proepisternal seta is present (Fig. 23) in the five Afrotropical species described by Burla (1954) and Lamb (1914) and in a possibly undescribed Malagasy species (S.F. McEvey, pers. obs.); the fore femora of males with numerous strong setae below; in many species the fore legs are bicoloured: the femur, tibia and metatarsus are entirely or largely black, the remaining tarsal segments and coxa white, the other legs usually pale yellowish brown; the coxa is also distinctly longer than in many other drosophilids; the wing tip often has a milky white macula (coincident with a region denude of microtrichia; the costal wing vein (*C*) reaches vein R_{4+5} and is darkened in Afrotropical species (*Ch. yvettae*, not examined). *Chymomyza* species are often collected near freshly cut timber, but Burla (1954) notes that they do not feed exclusively on tree sap and upon examination of the gut contents of *Ch. mafu* Burla, 1954, noted the presence of grey-brown fungal spores. The biology and immature stages otherwise remain unknown. Identification keys including most of the Afrotropical species were provided by Burla (1954:15) and Okada (1976).

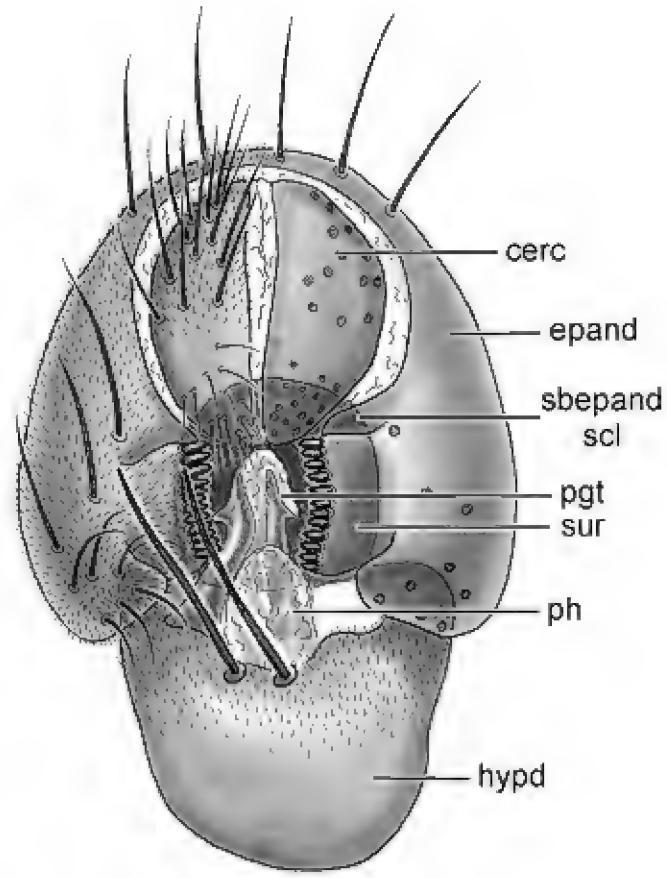
***Dettopsomyia* Lamb** (Drosophilinae)**.** A genus of 13 described species, occurring in all zoogeographical regions, except Antarctica. Four species occur in the Afrotropics, distributed in Cameroon, Côte d'Ivoire, Kenya, Seychelles, South Africa and Uganda. No additional undescribed species are known. *Dettopsomyia* are small flies (body length: *ca* 2 mm), with complex thoracic patterning (Fig. 18); the antennal arista is plumose and the antennal bases widely separated by a large, bulbous facial carina; the distal costal incision (subcostal break) is exceptionally deep (Fig. 55) and before the subcostal break the costal vein (*C*) protrudes and is thickened, blackened and bears two strong setae (Fig. 55); the second and third costal sectors are subequal (C-index *ca* 1.0); acrostichal setulae in 2 rows (*De. formosa* – type species of the genus from Seychelles, with distinctive patterned wing (Fig. 55), 4 rows (*De. nigrovittata* (Malloch, 1924) and *De. woodruffi* Takada, 1990) or 6 rows (*De. bombax* (Burla, 1954)); dorsocentral setae with 2 pairs (*De. nigrovittata* and *De. woodruffi*), or 3 pairs (*De. bombax*). In *De. formosa* all fronto-orbital setae are inserted very far forward (Fig. 29) while in *De. nigrovittata* the arrangement is less extreme (as in Figs 18, 28). *Dettopsomyia nigrovittata*, a widespread subtropical species, has been collected in large numbers on rotting stems of banana plants. The biology and immature stages otherwise remain unknown. An identification key including three of the Afrotropical species was provided by Okada (1982).

***Dichaetophora* Duda** (Drosophilinae)**.** A genus of 67 described species, occurring in the Afrotropical, Australasian, Oriental and Palaearctic Regions. Five described species are recorded from the Afrotropics, but Tsacas (1990: 139) excluded *Di. suruku* Burla, 1954, distributed in Central Africa, Madagascar and islands of the Indian Ocean and at least five undescribed species are known from Madagascar (Grimaldi *et al*. 2000: 130). "*Dichaetophora* was established as a subgenus of *Drosophila* by Duda (1940), based on the single species, *Drosophila aberrans* Lamb, from Seychelles. The original diagnostic characters for this subgenus were the anterior dorsocentral setae minute or absent, as in *Mycodrosophila*, but the portion of costal vein proximal to the subcostal break neither thickened nor dark" (Hu & Toda 2002: 91). When Hu & Toda (2002: 91) commenced their cladistic analysis and generic revision of *Dichaetophora* "… the four known named and one unnamed species of *Dichaetophora* [were] all from the Ethiopian Region, and 42 species of *Nesiodrosophila* [were] distributed in Asia (26), New Guinea (10), Australia (7), Micronesia and Madagascar (one species each): *N. lindae* is distributed over

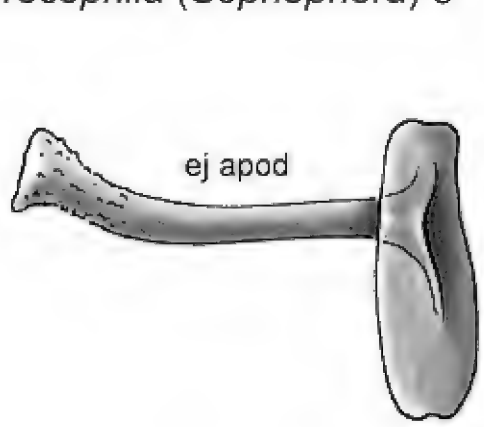
the first four of these areas." Duda (1940) established *Dichaetophora* as a *Drosophila* subgenus for Lamb's (1914) unusual species *Drosophila aberrans* from Seychelles. Wheeler & Takada (1964: 238) established the genus *Nesiodrosophila* for a species of the Australasian Region. In the years that followed, 35 species were added to *Nesiodrosophila* and just three (all Afrotropical) to *Dichaetophora*. In a careful cladistic analysis, Hu & Toda (2002) demonstrated that the *Lordiphosa tenuicauda* species-group clades and the *Dichaetophora* + *Nesiodrosophila* clade resolved at a similar level to other genera, warranting generic re-classification. *Nesiodrosophila* was synonymised with *Dichaetophora* and the genus was subdivided into three new species-groups (Hu & Toda 2002) and a fourth was added later (Hu & Toda 2005). All four Afrotropical species are now classified in the large *agbo* species-group of *Dichaetophora* (43 species, mainly Oriental/Palaearctic and Australasian Regions), the *D. tenuicauda* species-group has 10 Palaearctic/Oriental species and the small *D. acutissima, sinensis* and *trilobita* species-groups have four to six each. Hu & Toda (2002) characterise the *D. agbo* species-group: (a) longest axis of eye distinctly oblique to body axis; (b) profile line of frons from base to ptilinal fissure nearly straight; (c) posterior portion of cibarial dorsal wall parallel-sided; and (d) surstylus lacking pubescence. Many species of *Dichaetopora* have a white-pruinescent transverse fascia across the lower face. The biology and immature stages remain unknown. An identification key



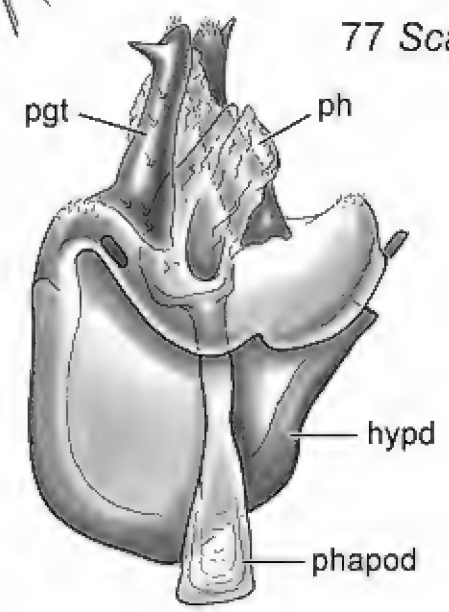
75 *Drosophila* (*Sophophora*) ♂



77 *Scaptodrosophila* ♂



76 *Drosophila* (*Sophophora*) ♂



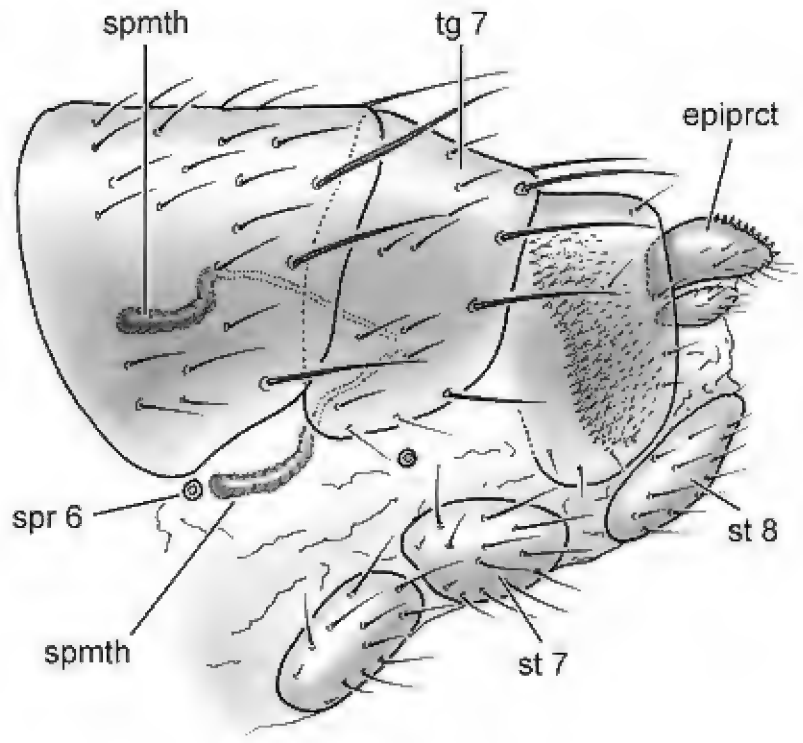
78 *Scaptodrosophila* ♂

Figs 106.75–78. Male terminalia of Drosophilidae: (75) epandrial complex of *Drosophila* (*Sophophora*) sp., caudal view; (76) same, ejaculatory apodeme, lateral view; (77) epandrial complex of *Scaptodrosophila* sp., caudal view; (78) same, terminalia (without epandrium), frontolateral view.

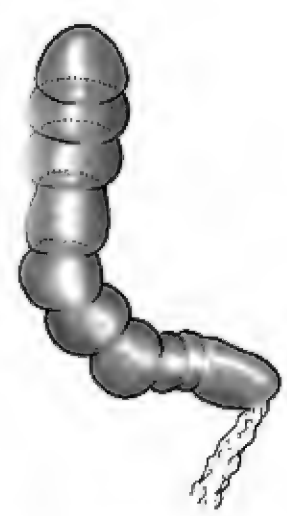
Abbreviations: cerc – cercus; ej apod – ejaculatory apodeme; epand – epandrium; epand lb – epandrial lobe; hypd – hypandrium; pgt – postgonite; ph – phallus; phapod – phallapodeme; prens – prensisetae; sbepand scl – subepandrial sclerite; sur – surstylus.

including all the Afrotropical species has not been published, but Burla (1954: 103) provided a character table diagnostically useful for *Di. aberrans*, *Di. agbo* (Burla, 1954), *Di. suruku* and an undescribed Côte d'Ivoire species.

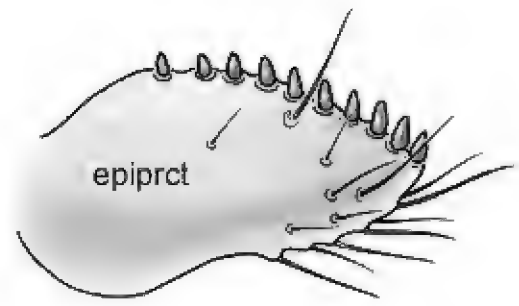
***Drosophila* Fallén** (Drosophilinae)**.** The largest genus of the family, with *ca* 1,235 species, although this number varies according to the classification adopted. There are *ca* 892 species if the problematic subgenus *Sophophora* is removed – note that *Drosophila melanogaster* is the type species of subgenus *Sophophora*, not of *Drosophila sensu stricto* and its placement within the genus *Drosophila* renders the genus paraphyletic. *Drosophila* species occur in all zoogeographical regions, except Antarctica, with 161 species occurring throughout the Afrotropics. Many additional undescribed species are known and many no doubt remain to be discovered in remaining rainforests of Central Africa and Madagascar. The genus is divided into subgenera, larger ones of which are divided into species-groups (although not all species are classified as such, e.g., Tsacas *et al*. 1981: 219, tables 1, 4). The Afrotropical Region



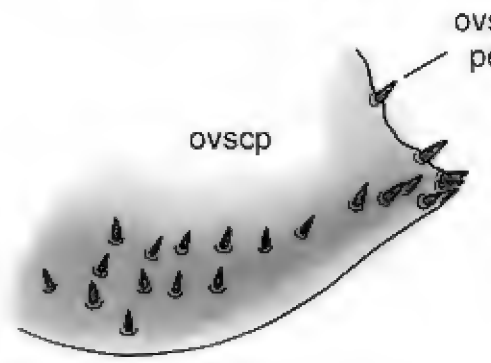
79 *Leucophenga* ♀



80 *Leucophenga* ♀

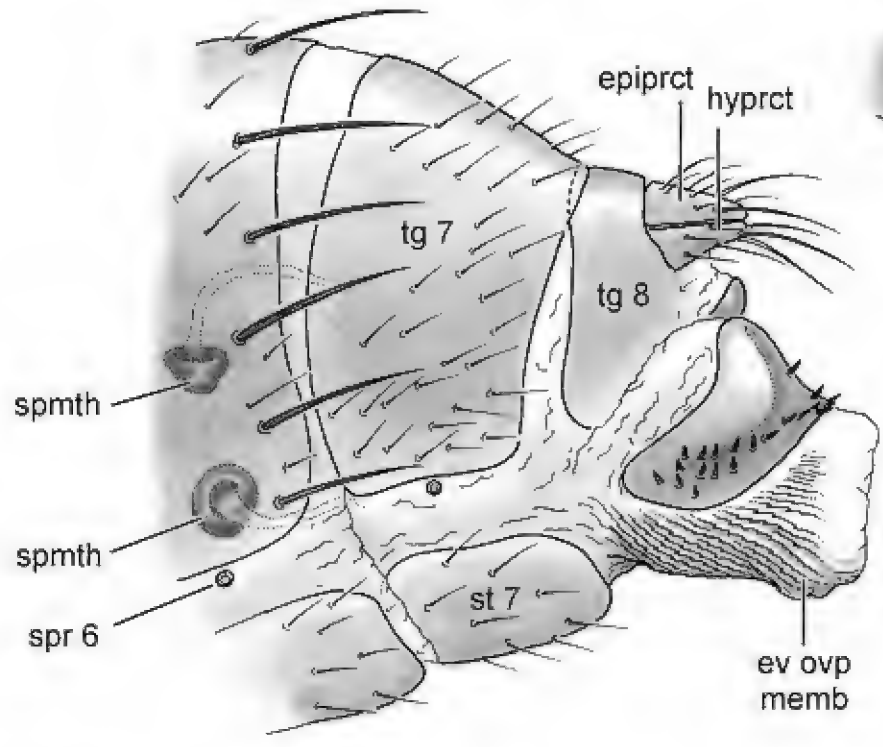


81 *Leucophenga* ♀



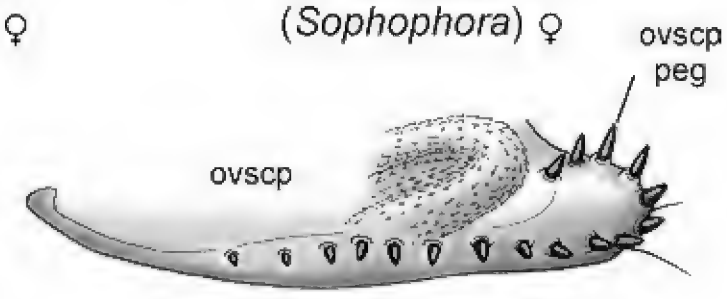
83 *Drosophila* (*Sophophora*) ♀

84 *Drosophila* (*Sophophora*) ♀



82 *Drosophila* (*Sophophora*) ♀

85 *Scaptodrosophila* ♀

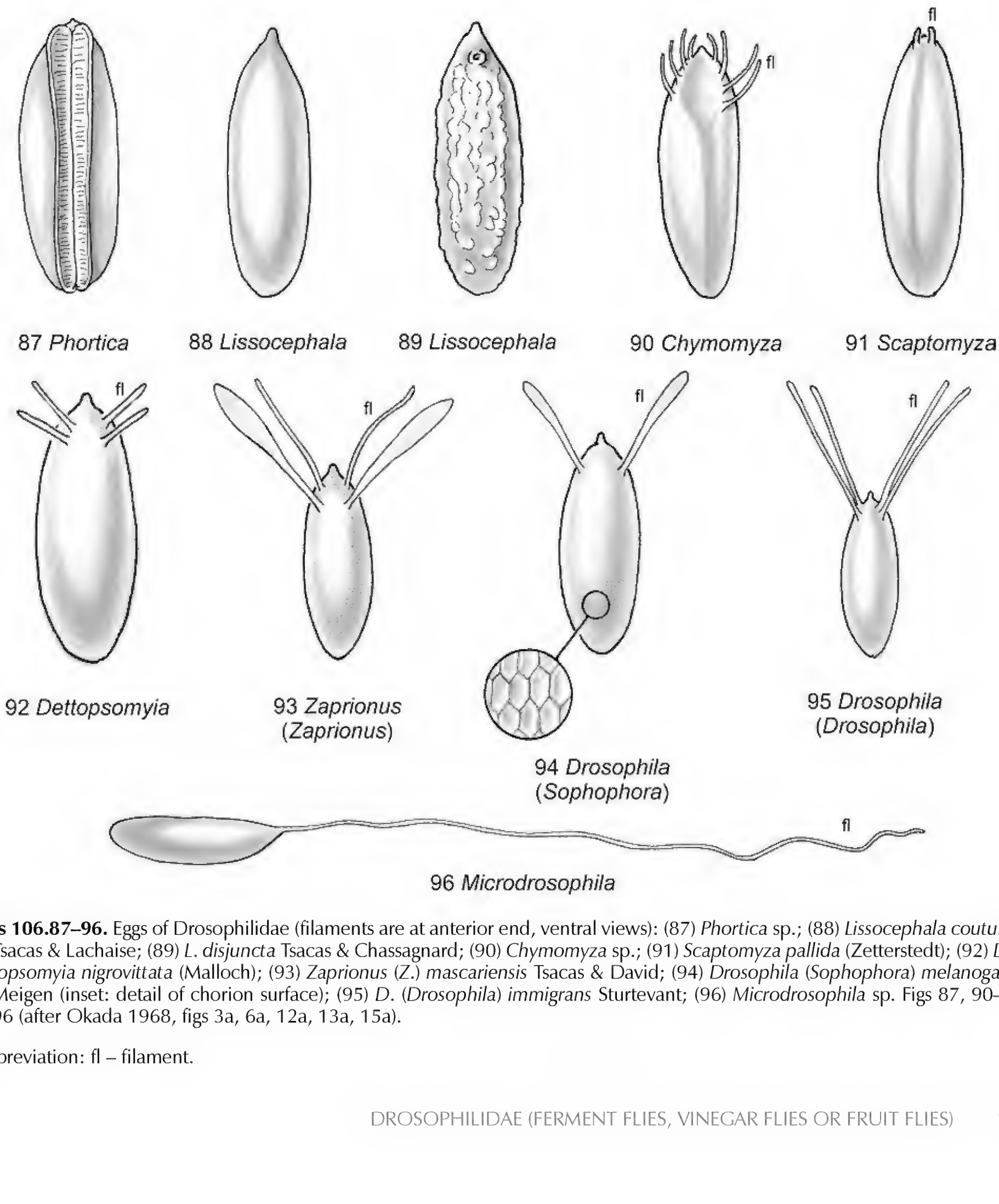


86 *Scaptodrosophila* ♀

Figs 106.79–86. Female abdomens and terminalia of Drosophilidae: (79) terminal segments of abdomen of *Leucophenga* sp., lateral view; (80) same, spermatheca, lateral view; (81) same, epiproct, lateral view; (82) terminal segments of abdomen of *Drosophila* (*Sophophora*) sp., lateral view; (83) same, oviscape (sternite 8), lateral view; (84) same, spermatheca, lateral view; (85) spermatheca of *Scaptodrosophila* sp., lateral view; (86) same, oviscape, lateral view.

Abbreviations: epiprct – epiproct; ev ovp memb – eversible ovipositor membrane; hyprct – hypoproct; ovscp – oviscape; ovscp peg – oviscape peg; spmth – spermatheca; spr – spiracle; st – sternite; tg – tergite.

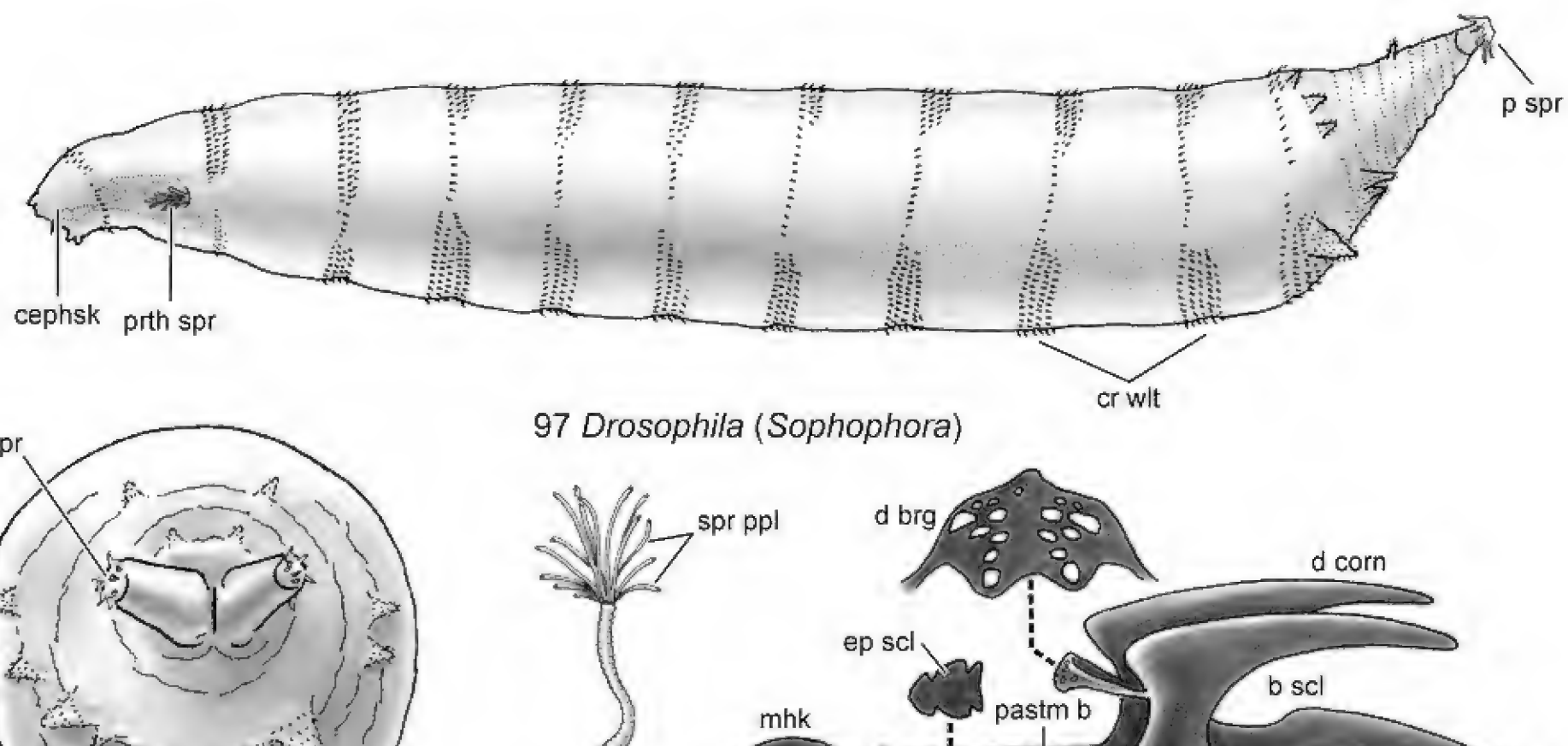
has three subgenera: *Drosophila sensu stricto*, *D.* (*Dorsilopha*) and *D.* (*Sophophora*), the second of these represented only by the virtually cosmopolitan, highly polyphagous species *D.* (*Do.*) *busckii* (native to Oriental South-east Asia; imaged by McEvey 2017*b*). *Drosophila sensu stricto* is represented by 64 species in the Afrotropics, seven of which are widespread species (Brake & Bächli 2008: 40). *Drosophila sensu stricto* is recognised by the prominent facial carina with a flattened margin; micro-pubescent compound eyes; the antennal arista with dorsal and ventral branches (Figs 43, 45); and usually with two strong vibrissae (Figs 20, 34). The most notable aspect of the Afrotropical *Drosophila sensu stricto* fauna is the *D.* (*D.*) *simulivora* species-group; an endemic lineage of six described species, the larvae of which are aquatic to semi-aquatic and predatory on nematoceran larvae and the gelatinous egg masses of other insects (Tsacas & Disney 1974). Common and widespread introduced species associated with human habitats are: *D.* (*D.*) *funebris* (F., 1787) (see Figs 19, 20), *D.* (*D.*) *hydei* Sturtevant, 1921 (McEvey 2017*a*, fig. 6), *D.* (*D.*) *immigrans* Sturtevant, 1921 (McEvey 2017*a*, fig. 5; McEvey *et al*. 1988, fig. 15) and *D.* (*D.*) *repleta* Wollaston, 1858 (three *Drosophila* species frequently sampled in Southern Africa are: *D.* (*D.*) *adamsi* Wheeler, 1959 (Figs 43, 63), *D.* (*D.*) *nasuta* (Fig. 74) and *D.* (*D.*) *punctatonervosa* Frey, 1954 (Figs 34, 62). The subgenus *D.*



Figs 106.87–96. Eggs of Drosophilidae (filaments are at anterior end, ventral views): (87) *Phortica* sp.; (88) *Lissocephala couturieri* Tsacas & Lachaise; (89) *L. disjuncta* Tsacas & Chassagnard; (90) *Chymomyza* sp.; (91) *Scaptomyza pallida* (Zetterstedt); (92) *Dettopsomyia nigrovittata* (Malloch); (93) *Zaprionus* (*Z.*) *mascariensis* Tsacas & David; (94) *Drosophila* (*Sophophora*) *melanogaster* Meigen (inset: detail of chorion surface); (95) *D.* (*Drosophila*) *immigrans* Sturtevant; (96) *Microdrosophila* sp. Figs 87, 90–92, 96 (after Okada 1968, figs 3a, 6a, 12a, 13a, 15a).

Abbreviation: fl – filament.

(*Sophophora*) includes the most intensively studied eukaryotic organism, *D.* (*S.*) *melanogaster*. It has spread globally, but is probably native to Central Africa. *Drosophila* (*Sophophora*) is a virtually global group that is more diverse in the Afrotropics than is *Drosophila sensu stricto*, with 91 species. The subgenus is clearly monophyletic, defined by the narrow facial carina, generally two pairs of vibrissae, dark abdominal tergal bands uninterrupted in the middle, the male commonly



Figs 106.97–108. Larval features of Drosophilidae: (97) habitus of third-instar larva of *Drosophila* (*Sophophora*) *melanogaster* Meigen, lateral view; (98) same, caudal view; (99) same, *D.* (*Dorsilopha*) *busckii* Coquillett; (100) larval prothoracic spiracle of *Drosophila* (*Drosophila*) *immigrans* Sturtevant, lateral view; (101) same, *Scaptomyza* sp.; (102) same, *Chymomyza* sp.; (103) cephaloskeleton of third-instar larva of *D.* (*S.*) *melanogaster*, lateral view; (104) larval mouthhook of *D.* (*S.*) *melanogaster*, lateral view; (105) same, *Scaptomyza pallida* (Zetterstedt); (106) same, *D.* (*D.*) *immigrans*; (107) same, *Microdrosophila* sp.; (108) same, *D.* (*D.*) *cogani* Tsacas & Disney. Figs 97–108 (after Okada 1968, figs 1, 6, 7, 13, 14, 66).

Abbreviations: an – anus; b scl – basal sclerite; cephsk – cephaloskeleton; cr wlt – creeping welts; d brg – dorsal bridge; d corn – dorsal cornu; den scl – dental sclerite; ep scl – epistomal sclerite; int scl – intermediate sclerite; mhk – mouthhook; p spr – posterior spiracle; pastm b – parastomal bar; prth spr – prothoracic spiracle; spr ppl – spiracular papillae; v corn – ventral cornu.

(although not invariably) with the fore tarsus bearing a comb of thick, black, tooth-like setae; and the egg with only two (as opposed to four), flattened/broadened filaments. The consensus of molecular evidence indicates that *D.* (*Sophophora*) is more early branching than *Drosophila sensu stricto* and many other drosophiline genera, although relegating this group as a separate genus is highly controversial. There are four species-groups of *D.* (*Sophophora*) in the Afrotropics, the *D.* (*S.*) *dentissima* and *D.* (*S.*) *fima* species-groups being endemic. The *D.* (*S.*) *obscura* species-group, which is diverse in the Northern Hemisphere, is represented in the Afrotropics by five species, with *D.* (*S.*) *microlabis* Séguy, 1938, known only from Kenya and Republic of Congo, at *ca* 2,500 m elevation. The *D.* (*S.*) *melanogaster* species-group (192 species globally) is the most diverse in the Afrotropics (45 species), there are 124 species of this species-group in the Oriental Region. Numerous identification keys are available, but a useful starting point is the key provided by Bock & Wheeler (1972). Before Grimaldi's (1990*a*) revision of the family Drosophilidae, *Scaptodrosophila* and *Hirtodrosophila* were treated as subgenera of *Drosophila* and much of the taxonomic literature relating to the Afrotropics precedes this re-classification. Burla, Chassagnard and Tsacas have, in hundreds of publications, described the majority of Afrotropical species of *Drosophila* during the last half of the twentieth century. Their works, together with those of Bächli, provide the best starting points for any taxonomic research in the region. Daniel Lachaise and Jean David have led teams who have, during the same time period, conducted numerous studies of the biology and ecology of *Drosophila* in the Afrotropics and islands of the Southern Indian Ocean, their works also number in the hundreds (see, for example, comprehensive list of plant-*Drosophila* associations in Lachaise & Tsacas (1984)). Their colleagues Lemeunier, Cariou, and Solignac and students, studied the molecular genetics and cytology (Lemeunier *et al*. 1986) of *Drosophila* strains established in the field largely by Lachaise and David or their students and maintained at the CNRS laboratories in Gif-sur-Yvette, France. Thousands of studies have been published around the world based on the *Drosophila* cultures and foundational work originating from the Gif laboratories under Jean David's leadership.

***Gitona* Meigen** (Steganinae)**.** A genus of 16 described species, occurring in the Afrotropical, Australasian, Oriental and Palaearctic Regions. New World species originally described in *Gitona* appear to belong to the non-Afrotropical genus *Rhinoleucophenga* Hendel. Eight species are recorded from the Afrotropics, distributed mainly in Madagascar, Mozambique, South Africa and Zimbabwe. One undescribed species is known from Lesotho. The genus is distinguished by the micro-pubescent antennal arista (Fig. 48) and is distinguishable from the genus *Cacoxenus* by the eight rows of acrostichal setae (as opposed to 10), the prominent facial carina (small in *Cacoxenus*) (Fig. 38), wing crossvein *bm–m* very faint (*dm* and *bm* cells confluent, or virtually so), as opposed to *bm–m* well-developed, the short costal vein (C) (weak beyond the apex of vein R_{4+5}, as opposed to strong to vein M_1) (Fig. 53) and the male terminalia with the surstylus fused to the epandrium and bearing a comb of blunt prensisetae (as opposed to an articulating surstylus with variable prensisetae. Little is known about their biology and the immature stages remain unknown. The Afrotropical species *G. gossypii* Séguy, 1933 was described from the damaged head capsules of the cotton plant *Gossypium* (Malvaceae). The larvae of *G. ethiopica* and *G. pauliani* are stem-borers on *Phytolacca dodecandra* in Ethiopia (Tsacas & Teshome 1981). The Palaearctic species *G. distigma* Meigen, 1830 is frequently cited as aphidophagous, but the evidence is weak (Ashburner 1981: 400). *Gitona distigma* has become a major pest of Drumstick tree, *Moringa oleifera* Lam. (Moringaceae) in India, the tree is widely cultivated for young seed pods and leaves, used for food and for traditional medicines. The fly pest has acquired the vernacular name "Drumstick pod fly" and is reported to have caused up to 70% production loss by infesting from the beginning of fruit initiation (Math *et al*. 2014 and works cited therein). An identification key for the Afrotropical species is not available.

***Hirtodrosophila* Duda** (Drosophilinae)**.** A genus of 177 described species, occurring in all zoogeographical regions, except Antarctica (Brake & Bächli 2008: 126, 21 described since 2008). Only five described species are recorded from the Afrotropics, distributed in Central Africa and islands of the Indian Ocean (Burla 1954). The species are nearly always restricted to fungal growths and are never taken in fruit traps and rarely in Malaise traps, many species no doubt await discovery because surveys focused on mycophagous drosophilids in Central Africa have been lacking and at least ten undescribed species are known from short periods of fieldwork in Madagascar and Southern Africa (S.F. McEvey, pers. obs.). The genus is probably paraphyletic with respect to *Mycodrosophila*, *Paramycodrosophila* and *Zygothrica*, all of which aggregate at fungi. *Hirtodrosophila* comprises typically, small, pale flies with a small, narrow facial carina, the scutum has faint fasciae or none and some species have long setulae on the antennal scape. The biology and immature stages remain unknown, except that larvae are invariably found in the fungus upon which adults swarm; and collected fungus will sometimes yield adult flies. An identification key including the Afrotropical species is unavailable, good starting points for taxonomic studies are nevertheless provided by Bächli (1974) and Burla (1954).

***Hypselothyrea* de Meijere** (Drosophilinae)**.** A genus of 35 described species, occurring in the Afrotropical, Australasian and Oriental Regions. The genus is subdivided into three subgenera: *Hypselothyrea sensu stricto*, which has a strongly upturned scutellum and no acrostichal setae; *H.* (*Deplanothyrea* Okada), without the upturned scutellum and with acrostichal setae (Okada 1980); and *H.* (*Baechlia* Papp) with frons and scutum granulated. The genus is represented in the Afrotropical Region by three described species: *H.* (*H.*) *africana* Papp, 2004, described from Guinea; *H.* (*D.*) *notabilis* (Lamb, 1914), from Seychelles; and *H.* (*D.*) *zulu*, from South Africa. Chassagnard *et al*. (1998) reported the presence of an additional three undescribed *H.* (*Deplanothyrea*) species from Malawi and Nigeria and a fourth undescribed species of *Hypselothyrea sensu stricto* is not uncommon in Madagascar. *Hypselothyrea sensu stricto* possess a slender and distinctly upturned scutellum, this character, together with their ant-like appearance and their usually slender, diminutive, or patterned wings make the genus one of the most easily recognised in the family. As knowledge of the genus expands, additional species (Bock 1982; Okada 1980; Papp 2004, 2009) and the subgenera *H.* (*Baechlia*) and *H.* (*Deplanothyrea*) have been added. Species of both subgenera possess flat (not upturned) scutella, thus neutralising the diagnostic value of the upturned scutellum trait and resulted

in the need for a more elaborate suite of diagnostics to isolate *Hypselothyrea* from the three taxa which are regarded as its closest congeners: *Liodrosophila*, *Jeannelopsis* and *Tambourella* Wheeler. Papp's (2004, 2009) studies are the most recent and comprehensive. He emphasised the "… distinct, medially flat (in profile nose-like) facial carina" of all *Hypselothyrea* species (Papp 2009: 39). *Hypselothyrea* species lack postocellar setae, have the basal abdominal segments constricted ("ant-like") and possess a sharply demarcated "frontal shield" (e.g., Lamb 1914: pl. 19, fig. 14). The genus is close to *Liodrosophila*, from which it differs in having a single postpronotal and a single katepisternal seta. In common with *Liodrosophila*, species of *Hypselothyrea* have "… rather sharply pointed oviscapes and [usually] a row of short black spines on the anteroventral surface of fore femur …" (Papp 2004: 271). The subgenus *H.* (*Baechlia*), with very distinctive wings is restricted to the Oriental Region and the genus *Tambourella* is restricted to the Australasian Region. Unlike *Jeannelopsis*, all Afrotropical *Hypselothyrea* species possess shiny black abdomens. Except in the tropical parts of the Australasian and Oriental Regions and interestingly in Madagascar, specimens are rarely encountered. Papp (2004) has shown that apterous species of the genus occur as bi-catch when coleopterists collect by sieving forest soils. The biology and immature stages remain unknown. Identification keys to Afrotropical species were provided by Papp (2004, 2009).

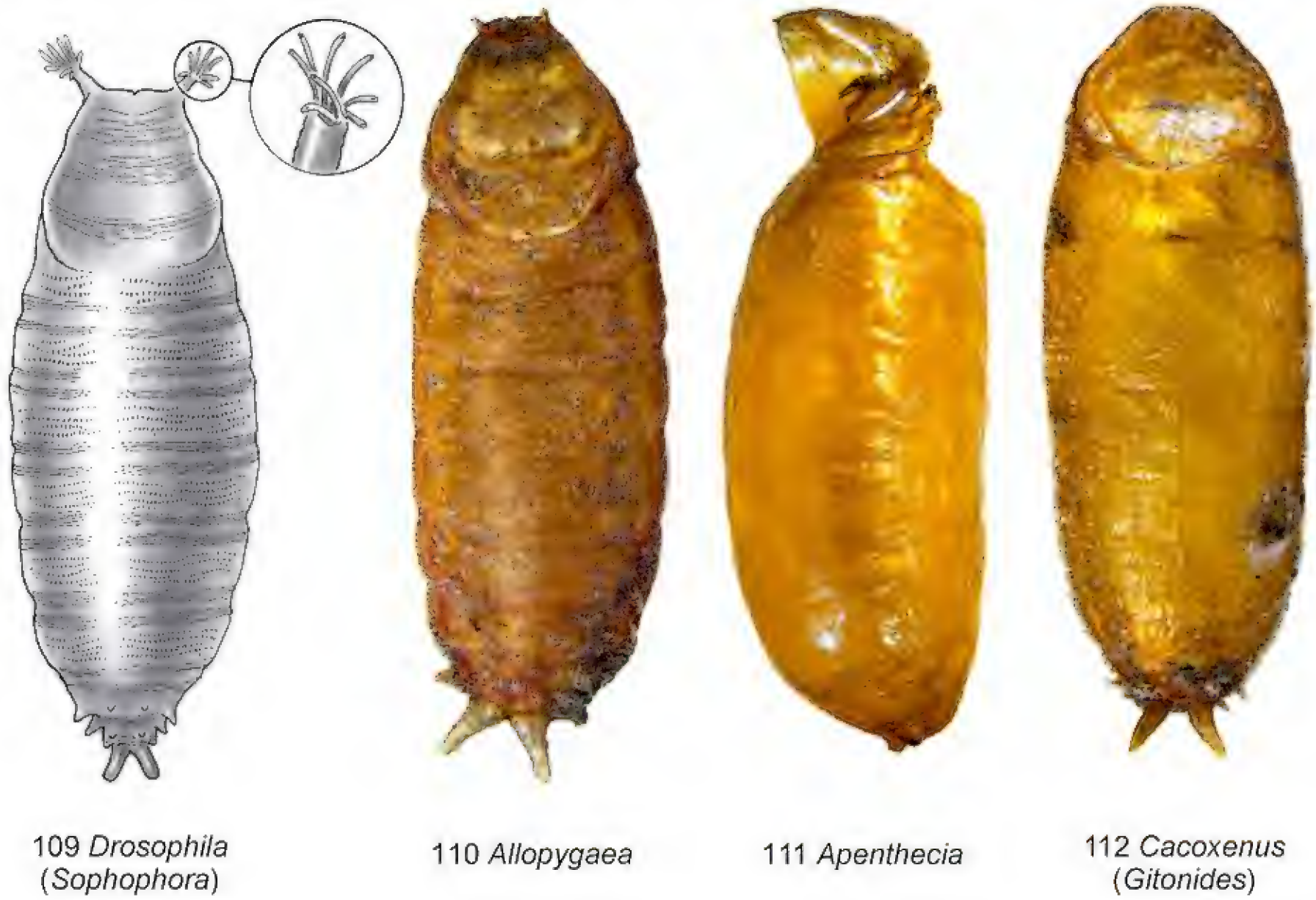
***Jeannelopsis* Séguy** (Drosophilinae)**.** A genus (Fig. 8) established for the single species, *J. mirabilis*, described from Kenya with, among other things, aberrant wing venation: multiple crossveins connect vein R_{2+3} to the costal vein (C) across the marginal cell (Fig. 58). Three additional species were added to the genus (Tsacas 1990), but while closely resembling *J. mirabilis* in many respects, they entirely lack the distinctive wing venation (Figs 56, 57). When describing the two South African species *J. aneura* Tsacas, 1990 (Fig. 56) and *J. zophoptera* Tsacas, 1990 (Fig. 57), Tsacas (1990) did not draw comparison with the very similar genus *Dichaetophora* then known as *Nesiodrosophila* (see comments under *Dichaetophora*). He did, however, transfer Burla's (1954) *Drosophila* (*Dichaetophora*) *suruku* Burla, 1954 to *Jeannelopsis*. Unknown to Tsacas (1990), Okada (1983) had already found very little difference between *Jeannelopsis* and *Nesiodrosophila* (= *Dichaetophora*). It seems likely that a detailed study of a representative range of the *ca* 60 *Dichaetophora* species and all species of *Jeannelopsis* will conclude that they are congeneric. For many decades *Jeannelopsis* was treated as endemic to the Afrotropical Region, but several specimens resembling *J. aneura* are known from Thailand (G. Bächli, pers. comm. 2021; unpubl.). Not only does this mean that *Jeannelopsis* is not endemic to the Afrotropics, but also that it cannot be regarded as an autochthonous Afrotropical group biogeographically isolated from Oriental *Dichaetophora*. The biology and immature stages remain unknown. An identification key to Afrotropical species is unavailable, but the three known Afrotropical species are readily distinguished from wing form (Figs 56–58).

***Leucophenga* Mik** (Steganinae)**.** A genus of 267 described species, occurring in all zoogeographical regions, except Antarctica, 64 of which have been described from China since 2008 (Bächli 2021; Brake & Bächli 2008: 265; see numerous works especially by Jia Huang with Hongwei Chen after 2008). *Leucophenga* is one of the largest genera in the Afrotropical drosophilid fauna: 69 (14%) of the 479 described Afrotropical drosophilids are *Leucophenga* and 26% (69/267 species) of the world's *Leucophenga* species are Afrotropical. The 69 Afrotropical species are distributed throughout the continental Afrotropics and in the southern Indian Ocean islands. The seven species described by Adams (1905) have label data "Salisbury, Rhodesia, South Africa" which is geospatially equivalent to present day Harare, Zimbabwe (not South Africa). *Leucophenga bellula* (Bergroth, 1894) is not known from the Afrotropics (Bächli 1971) and is incorrectly listed as Afrotropical in Brake & Bächli (2008: 267). Thirty to forty additional undescribed species are known from Central and Southern Africa and from Madagascar (Bächli 1971; Chassagnard *et al*. 1997; S.F. McEvey, pers. obs.). *Leucophenga* have the antennal arista with several straight branches above and below (Figs 11, 39), the antennal postpedicel with short or long marginal setulae (Fig. 21) and the frons is narrow (Fig. 66), narrower in the male than in the female in several species. The facial carina is rudimentary or absent and the gena is usually narrow (Fig. 39), with one vibrissa (Fig. 39). The compound eye is large, red and bare (Figs 10, 11). All fronto-orbital setae are large, the posterior reclinate fronto-orbital seta is typically inserted closer to the inner vertical seta than to the proclinate fronto-orbital seta (Fig. 66). The acrostichal setae are arranged in numerous rows, with the prescutellar pair long and two strong katepisternal setae (Fig. 11). The scutellum has basal and apical scutellar setae only (without supernumerary scutellar setation) and a small proepisternal seta is present. The costal wing vein (C) reaching only to the apex of vein R_{4+5} or slightly beyond and the third costal sector has minute ventral peg-like spines (Fig. 67, arrowed). The male terminalia has the surstylus without prensisetae. In certain species there is strong sexual dimorphism and when few specimens are available, it can be difficult to associate males with females. In many species, males have striking silvery or whitish pruinescence on the mesoscutum (Fig. 10), the thorax or both. Species of *Leucophenga* are the only Afrotropical drosophilids having a broad white pruinescent transverse abdominal fascia (a distinctive characteristic restricted to males of certain *Leucophenga* species) (Fig. 5). Dark abdominal maculae (e.g., *L. perargentata* Bächli, 1971, Fig. 11) vary in extent, e.g., two discrete black abdominal maculae in one specimen may be present as a coalescing mark in a second conspecific specimen (see also figures in Bächli 1971). Many species are mycophagous, but host-specificity is not suggested by the available information. Very large aggregations of resting adults are occasionally encountered in small grottoes (e.g., hollowed logs, unused fire-hearths, abandoned cars and small caves), suggesting that these species have a cavernicolous tendency. Specimens of *Leucophenga* are most often collected in Malaise traps or by sweep-netting and are, due to their shape, posture and movement, also conspicuous among small Diptera on a light sheet. The immature stages remain unknown. An identification key to Afrotropical species was provided by Bächli (1971: 20), but nine additional species (mainly from Madagascar) were described by Bächli *et al*. (2005).

***Liodrosophila* Duda** (Drosophilinae)**.** A genus of 64 described species, occurring in the Afrotropical, Australasian, Oriental and Palaearctic Regions. Seven species are recorded from the Afrotropical Region, distributed in Kenya, Madagascar and South Africa and several undescribed species were listed by Okada (1974), from Madagascar. *Liodrosophila* are small

(body length: *ca* 2.0–2.5 mm), usually glossy black species, with a very large glassy, mirror-like ocellar triangle, sufficiently large that the frontal vittae are reduced to narrow furrows between the triangle and the orbits (Fig. 65), the latter also glassy. The lunular setae are reduced, the antennal arista is plumose and the anterior reclinate fronto-orbital (Fig. 37) and postocellar setae are small or minute. A single vibrissa is present and the gena is linear (Fig. 37). The mesoscutum is glassy black or dark brown (in Afrotropical species), with two, four or six rows of acrostichal setae, or these entirely absent and with two pairs of dorsocentral setae and no prescutellar setae. The scutellum is velvety and typically black and the inner face of the fore femur often has a row of short, black spinescent setae. The biology and immature stages remain unknown. Chassagnard *et al*. (1997) provided an identification key to four African species and Okada (1974) described three additional species from Madagascar.

***Lissocephala* Malloch** (Drosophilinae)**.** A genus of 32 described species, occurring in the Afrotropical, Australasian and Oriental Regions. Twenty-two species are recorded from the Afrotropics, distributed "… over all the African continent and on Réunion and Cape Verde Islands" (Tsacas *et al*. 1981: 221). These Afrotropical species represent a natural and endemic group and there is some evidence suggesting that the 10 Australasian and Oriental species are a separate lineage (Tsacas *et al*. 1981: 254). A number of undescribed species were mentioned by the late Daniel Lachaise. *Lissocephala* are generally small drosophilids (body length: 2–3 mm), with a shiny straw-yellow head and thorax and shiny black or dark abdomens. The females often have extended tapering abdomens, which are inserted deep into fig ostioles during oviposition (Lachaise 1977; Lachaise *et al*. 1982). The wing membrane in both sexes is darkened near the apex and often also along the fore-edge (Figs 59–61). The wing markings and the colouration of the mesoscutum and scutellum are useful starting points in species-level sorting. *Lissocephala* have the frons subshiny and uniform in texture, without depressed or dull lines on each side of the ocellar triangle and slightly projecting, visor-like or eaves-like, over the bases of the antennae (Fig. 64). The postocellar setae are small and the inner and outer vertical setae are well-developed (Fig. 64). The ocellar setae are long and the posterior reclinate and proclinate fronto-orbital setae are strong, the anterior reclinate fronto-orbital seta is minute inserted between the others. The face is carinate (the facial carina very well-developed, with sharp straight margins, the ventral margin ending abruptly), the antennal arista is plumose and one vibrissa is present (Fig. 64). All Afrotropical *Lissocephala* species have two postpronotal setae (one or two postpronotal seta(e) in Australasian and Oriental species, e.g., *L. fijiensis*



Figs 106.109–112. Puparia of Drosophilidae: (109) *Drosophila* (*Sophophora*) *melanogaster* Meigen, dorsal view (inset: detail of prothoracic spiracle); (110) same, *Allopygaea* sp.; (111) *Apenthecia* sp., lateral view (puparial caps partly detached); (112) *Cacoxenus* (*Gitonides*) sp., dorsal view. Fig. 109 (after Okada 1968, fig. 1), Figs 110–112 (© Trustees of the Natural History Museum, London).

Harrison, 1954 and *L. powelli* Carson & Wheeler, 1973 have one postpronotal seta, but *L. metallescens* (de Meijere, 1914) has two). The thorax has two pairs of postsutural dorsocentral setae and no prescutellar setae, two pairs of scutellar setae, two large katepisternal setae and the acrostichal setae are arranged in six or more rows. Wing vein R_{2+3} is not curved at the apex and the costal-index is low, often < 1.0 (Figs 59–61), the fringe of heavy setation in the third costal sector is almost entire (0.8–0.95) and the basal medial (*bm*) and discal medial (*dm*) cells are confluent (Figs 59–61). The anterior cubital cell (*cua*) is sometimes closed and the posterior branch of vein *CuA+CuP* is very weak (Figs 59, 61) or sometimes absent. The costal vein (*C*) reaches M_1, but is extremely weak in the last sector (Figs 59–61). Wing membrane markings (which are not sexually dimorphic) vary among Afrotropical *Lissocephala* species, but all have a darkening near the wing apex (Figs 59–61). The small costal cell (*c*) is often dark (except hyaline in the type species *L. unipuncta* Malloch, 1929 and *L. sosefi* Chassagnard & Tsacas, 1997), the marginal cell is usually darkened along the anterior edge (along the second costal sector) in Afrotropical species, except in *L. diola* Tsacas & Lachaise, 1979, *L. lebou* Tsacas & Lachaise, 1979, *L. sosefi* and *L. unipuncta*, for example and this darkening occurs to a variable extent adjacent to the third costal sector in the apex of the submarginal cell, e.g., extensively so in *L. kamundii* Chassagnard & Tsacas, 1997 and *L. rasplusi* McEvey & Lachaise, 1990, but much less so in *L. sosefi* and *L. unipuncta*. Malloch (1929: fig. 1) described and illustrated cell *cua* of *L. unipuncta* as complete (see also wing photograph of the same species by Duda (1940), as "*Drosophila bicolor*"), cell *cua* is incomplete in most other Afrotropical *Lissocephala* species (e.g., Figs 59–61) and the cell is absent altogether in those species examined from outside the region (e.g., *L. fijiensis*, *L. metallescens* and *L. powelli*). The genus is closely associated in the Afrotropical Region with the syconia of *Ficus* where they breed. After the reproductive activity of fig wasps (Hymenoptera: Agaonidae) drosophilids can penetrate the fig syconium and exploit the resources within. There is a well-documented succession of species: firstly, *Lissocephala* species and secondly a less orderly sequence of numerous *Drosophila* (*Sophophora*) and *Zaprionus* species (Lachaise *et al*. 1982). "Fig-breeding drosophilids are specialised to a particular period of the successional stage. The *Lissocephala* species oviposit in the green immature syconium while the *Drosophila* (*S.*) *fima* group species oviposit in late ripe fallen figs. Opportunistic *Drosophila* (*Sophophora*) and *Zaprionus* species oviposit in the intervening period, separating both specialist groups. The last *Drosophila* (*Sophophora*) emerge from the dry remains of the receptacle on the ground … The specialization pattern in the succession appears to be similar regardless of the fig species…" (Lachaise *et al*. 1982: 145). The smooth-surfaced eggs of, for example, *L. couturier* Tsacas & Lachaise, 1979, which are laid internally compared to the unusually rugose chorion of *Lissocephala disjuncta* eggs, which are laid externally on figs has been the object of various ecological and evolutionary studies (e.g., Lachaise & McEvey 1990, Figs 88–89). Larval morphology, however, remains unknown. Identification keys have been provided for some species by Tsacas & Lachaise (1979) and Tsacas & Chassagnard (1981).

***Luzonimyia* Malloch** (Steganinae)**.** A small, distinctive genus of eight described species, occurring in the Afrotropical, Australasian and Oriental Regions. Five undescribed Afrotropical species are known from Madagascar and South Africa (Tsacas 1990). The first report of the genus in the region was based on a single specimen swept near Johannesburg and determined as *L. nigropuncta* Malloch, 1929 (McEvey *et al*. 1988), but following re-examination this specimen is now regarded as undescribed. *Luzonimyia* has the antennal arista micro-pubescent (Fig. 46), the head and thorax are distinctively cinerous or charcoal grey pruinescent, caused by a dense micro-pilosity (Figs 15, 68), the face is not carinate and the ocellar setae are small and inserted adjacent to the anterior ocellus (Fig. 30). All three fronto-orbital setae are large, the proclinate fronto-orbital seta is inserted in front of (and in line with) the reclinate fronto-orbital setae (Fig. 30) and the vibrissae are small (Fig. 30). There are two pairs of dorsocentral setae, the prescutellar setae are very large, inserted anteriad to the level of the posterior dorsocentral seta (Fig. 68). The basal medial (*bm*) and discal medial (*dm*) wing cells are confluent and the costal vein (*C*) reaches vein R_{4+5}. The legs are stramineous yellow (Fig. 15). A specimen of the Australian species *L. cineracea* Bock, 1982 was reared from a larva found living among psylloid-like bugs on *Eucalyptus* leaves in Sydney and on another occasion five adults were swept from blossom and psyllid lerp-covered *Eucalyptus* foliage 5–6 m above the ground. Species of this genus have not been taken at fruit-baits or at fungi. These observations suggest that *Luzonimyia* species have larvae that are predaceous on or inquiline with the early stages of hemipterous insects. The biology and immature stages otherwise remain unknown.

***Microdrosophila* Malloch** (Drosophilinae)**.** A genus of 77 described species, occurring in all zoogeographical regions, except Antarctica. Four described species are recorded from the Afrotropics, described from Côte d'Ivoire and Uganda and *ca* nine additional undescribed species are known from Madagascar and South Africa. *Microdrosophila* have the antennal arista plumose (Fig. 27), the breadth of the frons is considerably greater than the length and the anterior reclinate fronto-orbital seta is small, minute, or indistinguishable from the adjacent macrochaetae. Other cephalic setae are typically large and the proclinate and posterior reclinate fronto-orbital setae are inserted close together (Fig. 27). The periorbit is large and anteriorly much broadened, one vibrissa is present and typically very large, the second oral seta is small and fine, the gena is narrow, the compound eye with dense long pile and the ocellar setae inserted within the ocellar triangle (Fig. 27). The scutum is humped anteriorly (Fig. 12), typically with two pairs of dorsocentral setae, the anterior pair large and inserted close to the transverse suture (Fig. 12). In the Afrotropical species, *Mi. mamaru* (Burla, 1954) and *Mi. sexsetosa* (Duda, 1939), there are three pairs of large dorsocentral setae, the anteriormost presutural, the acrostichal setae are arranged in 6–8 rows, the prescutellar setae are absent, the scutellar setae are long and the posterior pair divergent, the anterior katepisternal seta is fine, the middle seta very small (ratio of anterior to posterior katepisternal setae *ca* 0.6) and there is one postpronotal seta. The wing tip is more or less pointed (Fig. 12) and the costal index is typically low, not over 1.5. The third costal sector has an extensive fringe of heavy setation, ranging from *ca* 0.8 to almost entire and the subcostal break is often deep. *Microdrosophila mabi* Burla, 1954 (eight rows acrostichal setae) and *Mi. korogo* Burla, 1954 (six rows acrostichal setae) have

two pairs of dorsocentral setae, whereas *Mi. mamaru* (7–8 dorsal aristal branches) and *Mi. sexsetosa* (5–6 dorsal aristal branches) have three pairs of dorsocentral setae. Very little is known about the biology of the genus and the immature stages remain unknown. They have been collected using various methods and they do not culture easily. An identification key to Afrotropical species is not available, but Burla's (1954) description of three of the four described Afrotropical species is a good starting point.

***Mycodrosophila* Oldenberg** (Drosophilinae)**.** A genus of 129 described species (Fig. 9), occurring in all zoogeographical regions, except Antarctica. There are 18 described Afrotropical species, all in *Mycodrosophila sensu stricto* (Brake & Bächli 2008; Burla 1954; David & Tsacas 1975; Grimaldi *et al*. 2000). An additional 20 undescribed species are known from Madagascar and Southern Africa, including several of the subgenus *My*. (*Promycodrosophila*) (species without a costal wing lappet), not previously recorded from the region. *Mycodrosophila* have a rounded or humped thorax and, in general, are black dorsally and white ventrally, with red eyes. The antennal arista is large and plumose, usually with one ventral branch (Fig. 41) and the facial carina is usually well-developed. A single vibrissa is present and the compound eyes are bare. The ocellar, postocellar and vertical setae are large and the anterior reclinate fronto-orbital seta small or minute (Fig. 24). The mesonotum is strongly rounded and humped (viewed in profile) and usually blackish and subshiny (Fig. 17). The scutellum is broadly rounded, dark, velvety or subshiny. The anterior dorsocentral setae are absent or greatly reduced and inserted close to the posterior dorsocentral setae (Figs 17, 24). The acrostichal setulae are in numerous rows and the prescutellar setae are absent. The basal scutellar setae are short and fine and the apical scutellar setae large and convergent. The costal wing vein (C) is darkened at the distal costal incision in *Mycodrosophila sensu stricto*, protruding as a blackened costal lappet (Fig. 50). The frons often has medial pruinescence, which is most striking when viewed at acute angles. The uppermost parts of the thoracic pleura, above the level of wing articulation, is usually black or dark brown, with a well-defined margin of demarcation separating the dorsal dark and ventral pale parts of the thorax and in some species the pleura is also dark and concolourous with a dark mesoscutum (Fig. 17). *Mycodrosophila* species are associated with fungi. They are desiccation sensitive and slow-moving. They are most frequently taken directly off, or in the vicinity of, bracket fungi and other fleshy fungal fruiting bodies, often under rotting logs in deeply shaded forests. Relatively few specimens are taken in Malaise traps, or in mushroom baits and even fewer are sampled in fruit-baits or come to light. The biology and immature stages otherwise remain unknown. An identification key to many of the Afrotropical species was provided by Burla (1954: 16).

***Neotanygastrella* Duda** (Drosophilinae)**.** A genus of 17 described species, occurring in the Afrotropical, Australasian, Neotropical and Oriental Regions. Five species are recorded from the Afrotropics, all from Côte d'Ivoire (Burla 1954). This small distinctive genus is closely related to *Chymomyza*. The dark fore femur and tibia contrast with the light fore tarsi, the anterior reclinate fronto-orbital seta is small and lateral, or slightly anterolateral to the anterior proclinate fronto-orbital seta (Fig. 35) and the male terminalia has long, setose epandrial lobes and postgonites. *Neotanygastrella* is distinguished from *Chymomyza* by the anterior reclinate fronto-orbital setae not so displaced anteriorly, the face long and bulging near the oral margin (as opposed to short and flat), the female oviscape with pegs (as opposed to fine setae) and wing vein R_{2+3} longer. As with *Chymomyza*, *Neotanygastrella* aggregate at tree wounds. The biology and immature stages otherwise remain unknown. An identification key to the five Afrotropical species was provided by Burla (1954: 15).

***Paraleucophenga* Hendel** (Steganinae)**.** A genus of 12 species, occurring in the Afrotropical, Oriental and Palaearctic Regions (Brake & Bächli 2008: 281; Zhao *et al*. 2009). A single Afrotropical species, *P. semiplumata* (Duda, 1939), was described from Uganda and re-described and illustrated by Bächli (1971). The species was later recorded from Cameroon and Nigeria by Tsacas (1980: 676) and Grimaldi *et al*. (2000) reported an undescribed species from Madagascar. *Paraleucophenga* are large flies (body length: *ca* 4–5 mm), with the abdominal tergites with silvery pruinescence, the ventral branches of the antennal arista are shorter than the dorsal branches, the scutellum has supernumerary setae (in addition to the four scutellar setae) and there are three strong katepisternal setae. The third costal sector of the wing is without ventral spinescent setation (Bächli 1971), as in *Leucophenga* and *Stegana*. The genus is distinguished by the scutellum bearing numerous setae along the margin (*i.e*., with more than two pairs of scutellar setae), it lacks the costal thorn-like spinules apparent in *Leucophenga* and *Stegana* and the male terminalia has the surstylus with a small comb of prensisetae and the postgonite also with a comb of teeth. Adult males fly around the heads of humans at forest margins, otherwise the biology and immature stages remain unknown. *Paraleucophenga semiplumata* was included in an identification key to Afrotropical *Leucophenga* and *Paraleucophenga* species provided by Bächli (1971: 20); other useful diagnostic information was given by Tsacas (2000)

***Phortica* Schiner** (Steganinae)**.** A genus of 153 species, occurring in all zoogeographical regions, except Antarctica. Six species are recorded from the Afrotropics, distributed in Central and Southern Africa. The genus was formerly classified as a subgenus of *Amiota* (see above), but is now treated as a genus with six subgenera (Brake & Bächli 2008: 282; Cao *et al*. 2011; Máca 2003): subgenus *P.* (*Allophortica* Máca) (four species, two Afrotropical: *P.* (*A.*) *fenestrata* Duda, 1939 and *P.* (*A.*) *vumbae* (Tsacas, 1990)); the subgenus *Phortica sensu stricto* (124 species, > 90% Asian; four Afrotropical: *P.* (*P.*) *africana* (Malloch, 1925), *P.* (*P.*) *flavithorax* Duda, 1939, *P.* (*P.*) *sexpunctata* (Séguy, 1938) and *P.* (*P.*) *sobodo* Burla, 1954); and the subgenera *P.* (*Sinophthalmus*), *P.* (*Ashima* Chen), *P.* (*Alloparadisa* Cao Cao, Wang, Gao, Prigent, Watabe, Zhang & Chen) and *P.* (*Shangrila* Cao, Wang, Gao, Prigent, Watabe, Zhang & Chen) (mostly Old World species). Flies in this genus have a pruinescent, maculated mesonotum, banded tibiae and very complex male terminalia with a narrow, U-shaped hypandrium, the surstylus lacking prensisetae, the phallapodeme is vestigial and gonopods/postgonites possess elaborate processes and spines. Like *Amiota*, males fly about the eyes of humans and other mammals and in several situations are also known to be intermediate hosts of Thelaziidae nematodes (Otranto *et al*. 2012). The biology and immature stages otherwise remain unknown. An identification key including all Afrotropical species is unavailable.

***Phorticella* Duda** (Drosophilinae)**.** A genus of 11 species, occurring in the, Afrotropical, Australasian, Oriental and Palaearctic Regions. Only a single species, *P.* (*Xenophorticella* Okada & Carson) *madagascariensis* Chassagnard & McEvey, 1997, has been reported from the Afrotropical Region. No additional undescribed species are known from the Afrotropics. The genus is divided into two subgenera: *Phorticella sensu stricto* (non-Afrotropical) and *P.* (*Xenophorticella*). *Phorticella* Duda, *Zaprionus* and the rare *Zaropunis* Tsacas have silvery white longitudinal fasciae on the scutum and frons (Figs 6, 7); *Zygothrica zaprionides* Tsacas has silvery white frontal fasciae only. The distinction between *Phorticella* and *Zaprionus* has always been vague. *Phorticella* species typically have: (a) a low orbito-index of *ca* 0.45–0.65 (*ca* 1.0 in *Zaprionus*; the index is the ratio of the proclinate fronto-orbital seta to posterior reclinate fronto-orbital seta distance and the proclinate fronto-orbital seta to inner vertical seta distance (McEvey 1990*a*); (b) minute cuneiform setae on the mid and hind tarsi absent in *Phorticella sensu stricto*, present in *P.* (*Xenophorticella*) and in *Zaprionus*; (c) ventral margin of epandrium truncate (pointed below in *Zaprionus*); and (d) hypandrium with two long submedian spines (1 or 2 short submedian spines in *Zaprionus*) (Okada & Carson 1983). Longitudinal striation is not restricted to these two genera and the condition has clearly evolved independently many times in the Diptera. Both drosophilid genera are, in many respects, closer to *Drosophila sensu stricto* than is the subgenus *D.* (*Sophophora*) (Grimaldi 1990*a*; Yassin *et al*. 2010). Several fasciate drosophilids that depart significantly from typical *Phorticella* and typical *Zaprionus* do not obviously belong in any other genera and were once ranked as *incertae sedis* (Wheeler 1981: 80) in Drosophilinae or grouped together in the *Drosophila* (*Drosophila*) *lineosa* species-group (Wilson *et al*. 1969). *Phorticella* (*X.*) *madagascariensis* has been collected at fruit-bait and is probably easily reared as a laboratory culture. The biology and immature stages otherwise remain unknown.

***Scaptodrosophila* Duda** (Drosophilinae)**.** A large genus of *ca* 298 species, occurring in all zoogeographical regions, except Antarctica (Brake & Bächli 2008: 194), being by far most diverse in the Australasian Region. There are 32 described species recorded from the Afrotropical Region, distributed throughout. The genus remains understudied in the region and numerous undescribed species await description from various countries, including Benin, Côte d'Ivoire, Madagascar, Mauritius, Republic of Congo and South Africa. Only one species is described from Madagascar, for example, although many undescribed species are known. *Scaptodrosophila* are commonly dark and typically have a short, squared, or narrow facial carina, prescutellar setae, three large katepisternal setae (as opposed to two), a well-developed female oviscape and male terminalia are distinctive (the phallus is simple and the postgonite has a row of fine sensilla trichodea (Figs 77, 78). The egg is also distinctive with six filaments. Many species develop in or visit flowers. The biology and immature stages otherwise remain unknown. Diagnostic information for 13 Côte d'Ivoire *Scaptodrosophila* species was provided by Burla (1954: 115, see under *Drosophila* subgenus *Pholadoris* Sturtevant); another five Seychelles species, some of which are now treated as widespread in the Afrotropics, were described together in surprisingly useful detail by Lamb (1914). A taxonomic study of the Afrotropical *Scaptodrosophila* fauna rests on a detailed knowledge of the species described in these two early studies.

***Scaptomyza* Hardy** (Drosophilinae)**.** A large genus of 263 species, occurring in all zoogeographical regions, except Antarctica. Three species are virtually cosmopolitan and 141 species (53%) are endemic to the Hawaiian Islands. Only 27 described species are recorded from the Afrotropics, and of those, nine are restricted to Tristan da Cunha Is., six others are also island endemics from Madagascar, Mauritius, Saint Helena Is. and Seychelles (Frey 1954; Kirk-Spriggs & Muller 2017: 229, fig. 9.55; McEvey 1990*a*). No additional undescribed species are known. The genus is divided into 17 subgenera, the monophyly and relationships of which need to be examined and are not applied here. The genus comprises slender species with elongated wings and rounded heads. One of the most distinctive features is the low number of acrostichal setae rows (in 2–4 rows; generally, in 6–8 rows in other drosophilids). The face is short, with a small facial carina, the compound eyes are rounded in lateral view, the antennal arista is plumose, one pair (rarely two) of vibrissae are present and the anterior reclinate fronto-orbital seta is small and lateral to the proclinate fronto-orbital seta. The mesonotum usually has diffuse longitudinal fasciae, varying from bold to (most often) faint and pruinescent. The male terminalia is typically complex, with a large, projecting pair of gonopods lateral to the postgonites and spine-like setae on the ventral portion of the cercus and/or ventral epandrial lobe (in addition to surstylus). The oviscapt is usually with stout marginal pegs and commonly with smaller pegs on the lateral face of the valve. Larvae are leaf- and stem-miners and adults can be very abundant in open habitats, such as grasslands and heath. The biology and immature stages otherwise remain unknown. An identification key for many, but not all, Afrotropical species was provided by Frey (1954).

***Stegana* Meigen** (Steganinae)**.** A genus of 246 described species, occurring in all zoogeographical regions, except Antarctica. Eight species are recorded from the Afrotropics, distributed in Central and Southern Africa. Compared to the closely related genus *Leucophenga*, *Stegana* is a relatively rare genus in the Afrotropics; three undescribed species are known from Madagascar and two from Malawi. *Stegana* is one of the most recognisable genera of the family globally. They are dark, brownish to blackish flies, with dark wings, that are characteristically flexed along the sides of body when at rest. The wing tip is pointed and veins R_{4+5} and M_1 are strongly convergent (Fig. 51), with thorn-like spinules on the costal vein (*C*), between the apices of veins R_{2+3} and R_{4+5} (Fig. 51, arrowed). The notum is slightly flattened, the frons flattened and long and one or more pairs of tarsi have longitudinal ctenidia. The genus is rarely collected with other drosophilids by baiting or sweeping, but more commonly in Malaise traps and by sweeping up and down trunks of wounded and decaying trees. Larvae probably feed on fungal mycelia under bark. The biology and immature stages otherwise remain unknown. An identification key to the eight Afrotropical species was provided by Tsacas & Chassagnard (1996).

***Zaprionus* Coquillett** (Drosophilinae)**.** A genus of 59 described species, occurring mainly in the Afrotropical Region, just 12 species found in other regions (Australasian, Oriental, Palaearctic) and *Z. indianus* Gupta, 1970 has spread to the Nearctic and Neotropical Regions. The 47 Afrotropical species are recorded throughout the continental Afrotropics and the islands of the southern Indian Ocean. Afrotropical *Zaprionus*

are all representatives of the subgenus *Zaprionus sensu stricto* and are almost all endemic. Of the 13 species occurring mainly in Madagascar, but also on other smaller Indian Ocean islands, five are endemic (Chassagnard & McEvey 1992). The subgenus *Z.* (*Anaprionus* Okada) includes 12 Australasian and Oriental species, none of which occur in the Afrotropics. Only *Z.* (*Z.*) *ghesquierei* Collart, 1937, *Z.* (*Z.*) *indianus* and *Z.* (*Z.*) *tuberculatus* Malloch, 1932 have spread (apparently in recent decades), out of the region (Chassagnard & Kraaijeveld 1991; Raspi *et al*. 2014). *Zaprionus* (*Z.*) *indianus* is an invasive species in the New World, spreading rapidly from a probable point of entry in Brazil in the 1990s (Vilela 1999) and reaching Ontario and Quebec in Canada within the past several years (Renkema *et al*. 2013). The genus is one of the most distinctive (Figs 6, 7, 22, 71–73) and ubiquitous of the Afrotropical drosophilids. The genus is most readily recognised by the silvery white longitudinal fasciae dorsally on the head and thorax (Figs 7, 71–73), but can also be distinguished as follows: the antennal arista is plumose (Fig. 22); the facial carina is very large (Fig. 22); a single vibrissa is present (Fig. 22); the fronto-orbital setae are all developed and in line, the posterior reclinate fronto-orbital seta is inserted slightly closer to the inner vertical seta than to the proclinate fronto-orbital seta (Fig. 22); the ocellar, vertical and postocellar setae are all developed (Fig. 22); the prescutellar acrostichal setae are small or only slightly enlarged; the posterior katepisternal seta is large only; and the male fore femur in typical species (e.g., *Z.* (*Z.*) *vittiger*) with a row of tubercles on the lower surface, each tubercle with large basal seta (Fig. 70). The form, number, and arrangement of tubercles, spines and nodules on the fore femur ventrally varies between species (Chassagnard 1996; Chassagnard & Tsacas 1993; Tsacas & Chassagnard 1990). The distinction between *Zaprionus* and the genus *Phorticella* has not been satisfactorily resolved (Bock 1982; Chassagnard & McEvey 1997; Grimaldi 1990*a*). Fruit-baiting surveys in the Afrotropics typically yield very large numbers of *Zaprionus* specimens, in contrast with the Australasian and Oriental Regions, which normally yield high diversity of *Drosophila* (*Sophophora*), *Drosophila sensu stricto* and *Scaptodrosophila* species and only rarely *Zaprionus*. The biology and immature stages otherwise remain unknown. An identification key to all species of the region is unavailable, but a key to the *Z.* (*Z.*) *vittiger* group-species (Chassagnard & Tsacas 1993), to the Malagasy species (Chassagnard & McEvey 1992); and to all species-groups, with detailed illustrations of femoral ornamentation and terminalia (Chassagnard 1989; Tsacas & Chassagnard 1990) have been published.

***Zaropunis* Tsacas** (Drosophilinae)**.** An endemic monotypic genus, with the single species, *Z. melanope* Tsacas, 1990, described from three specimens from Cameroon and Mozambique, with five additional badly damaged specimens recorded from Côte d'Ivoire and Republic of Congo (Tsacas 1990). No additional undescribed species are known. *Zaropunis* are small (body length: 2.0–2.3 mm), dark flies, with the frons with three narrow, white fasciae, two orbital and one medial, the latter extending from the facial carina ventrally to the ocellar callus. The relatively long anterior reclinate fronto-orbital seta is inserted closer to the proclinate fronto-orbital seta than to the posterior reclinate fronto-orbital seta and this seta is inserted closer to the inner vertical seta than to the proclinate fronto-orbital seta, *i*.e., orbito-index (McEvey 1990*a*) > 1. The facial carina is well-developed, rounded above and reaches the margin of the epistome. One very long, inwardly curved vibrissa is present, which is slightly longer than the inner vertical and ocellar setae. The scutum has four narrow, silvery-pruinescent fasciae and three pairs of dorsocentral setae, the anterior pair longer than the intermediate pair and presutural. Well-developed prescutellar setae are present, two pairs of scutellar setae, the basal shorter and convergent and two katepisternal setae. The fore and mid tibiae have an apical seta and the hind tibia a preapical seta. The male terminalia are very similar to those of *Zaprionus sensu stricto*. The biology and immature stages of the species remain unknown.

***Zygothrica* Wiedemann** (Drosophilinae)**.** A genus of 124 described species, occurring in the Afrotropical, Australasian, Neotropical and Oriental Regions, being extremely diverse in the Neotropics (Burla 1956; Grimaldi 1987), but with far fewer species in the Old World tropics (Grimaldi 1990*b*; Prigent & Toda 2006). Only two species are recorded from the Afrotropics: *Zy. africana* Grimaldi, 1990, described from Uganda and *Zy. zaprionides* Tsacas, 1990, from South Africa. Several undescribed species are known from Madagascar. Mostly boldly patterned, colourful flies, distinctive for the protruding, nose-like facial carina, the proboscis with a slender, long labium protruding beyond the oral margin and the small labellum. Species of the genus are associated with forest fungi, but the biology and immature stages otherwise remain unknown. No identification key to Afrotropical species is available.

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CRYPTOCHETIDAE 107

(Cryptochetid Flies)

Ashley H. Kirk-Spriggs and Emilia P. Nartshuk

Fig. 107.1. Females of *Cryptochetum* sp. (non-Afrotropical) (photograph © S.A. Marshall).

Diagnosis

Small- to minute-sized (body length: 2–4 mm), stout-bodied acalyptrate flies (Fig. 1), shiny black or metallic blue in colour, with broad, high head and clear, wide wings; antenna with postpedicel elongate and compressed; arista lacking in Old World *Cryptochetum* Rondani (short in the non-Afrotropical genus *Librella* McAlpine).

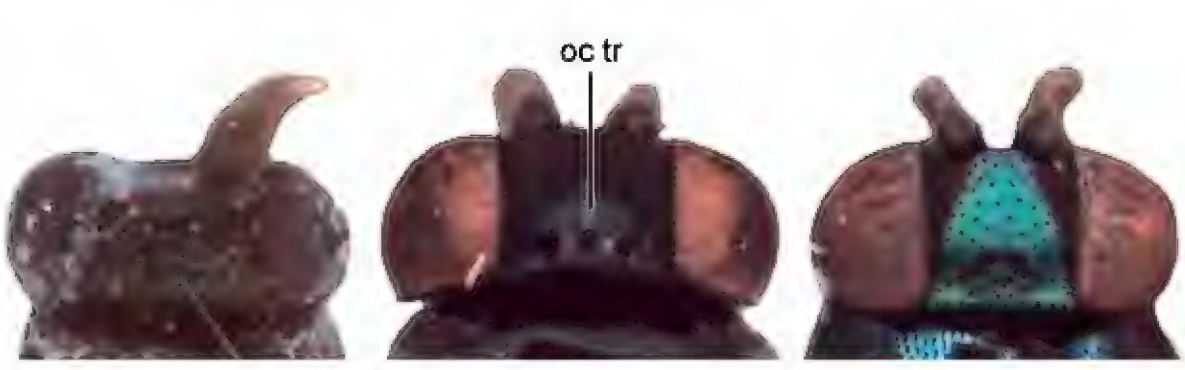
Head (Fig. 1) at least as broad as thorax, compressed from front to rear; frons virtually square in both sexes, shiny with large ocellar triangle; ocellar triangle usually occupying most of frons, differing in extent in four subgenera: in Afrotropical subgenera ocellar triangle either entirely filling frons (Fig. 2), short with sharply pointed apex (Fig. 3) or with wide, blunt apex (Fig. 4); major head setation scarcely distinguishable, but frons clothed in short setulae throughout; compound eye (Fig. 1) large, oval, occupying most of side of head, clothed in ommatrichia; 3 ocelli present (Figs 2–4); gena linear, or rarely high, with numerous short setulae; vibrissa absent; antenna large decumbent; scape and pedicel short, pedicel without notch on inner dorsal side, lacking usual outstanding dorsal setae; postpedicel large, oval and compressed, reaching lower margin on face, without dorso-basal tubule fitting into hollow in scape, surface usually uniformly pubescent; long arista absent, in *Cryptochetum* with short peg-like sensory process articulated on anterodistal part (considered

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2021. Manual of Afrotropical Diptera. Volume 3. Brachycera—Cyclorrhapha, excluding Calyptratae. *Suricata* 8. South African National Biodiversity Institute, Pretoria; pp. 2331–2337.

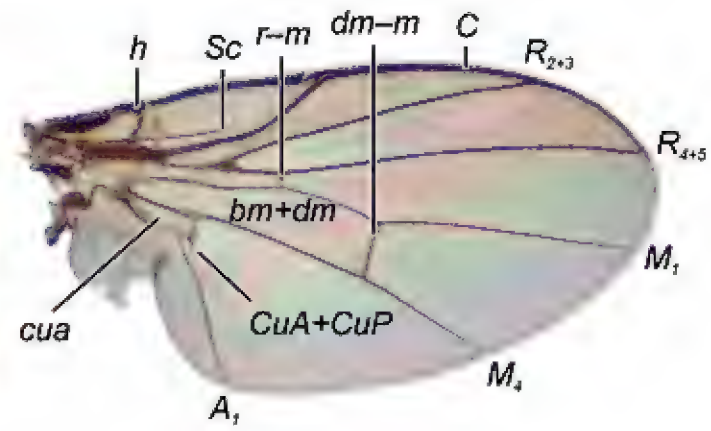
to be vestige of true arista); face convex with rather long and weakly raised medial carina that separates antennal foveae dorsally; proboscis and palpus short, palpus rather thick.

Thorax (Fig. 1) stout, convex dorsally; mesonotum devoid of strong setae, except towards lateral and posterior margins, clothed in numerous irregular setulae; postpronotum small, much compressed, positioned on vertico-anterior surface of thorax; anepisternum setulose, other parts of pleuron bare; prosternum large, bare, fused with propleuron, forming narrow, well-sclerotised precoxal bridge; anterior spiracle small, round. Scutellum unusually large, convex triangular with sharp margins laterally and apically, with pair of minute scutellar setae apically; subscutellum strongly developed. Wing (Fig. 5) hyaline, short and wide, with strong anal angle; membrane clothed in microtrichia; costal vein (*C*) setulose, extended slightly beyond apex of vein R_{4+5}, or to vein M_1, with 2 costal breaks: first just beyond humeral crossvein, second at end of subcostal vein (*Sc*); subcostal vein reaching costal vein (*C*), but weakened apically; cells *bm* and *dm* confluent, with crossvein *bm–m* absent; cell *cua* not fully demarcated; crossvein *r–m* present; crossvein *dm–m* far removed from posterior margin of wing; vein *CuA+CuP* reduced to short fold; vein A_1 developed, almost reaching wing margin; calypter rudimentary, not ciliate; halter short, knob usually black. Legs (Fig. 1) stocky, without outstanding setation; ventral apex of mid tibia with corona of short setae; hind tibia posterodorsally with velvety sensory macula.

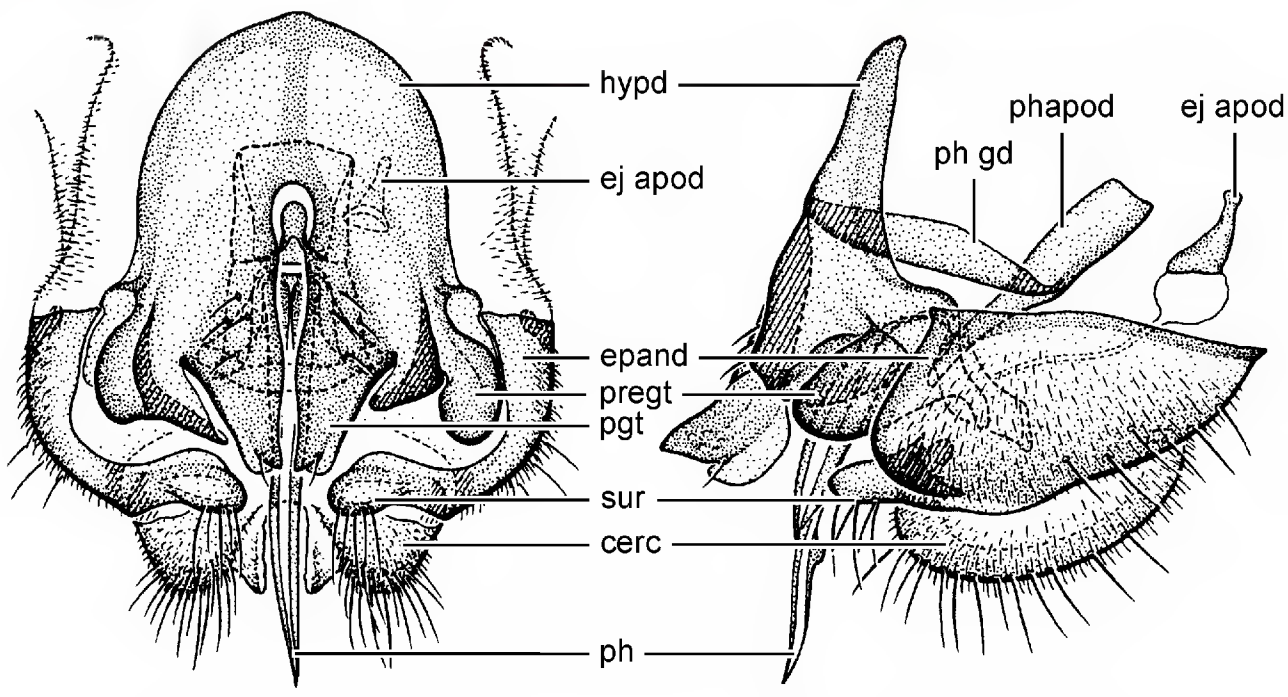
Abdomen (Figs 10, 11) short and broad, with 6 well-developed tergites in both sexes; tergites 1 and 2 partly fused (syntergite 1 + 2); sternites 1–5 much reduced, but sternite 6 in male (Fig. 10) and sternites 4 and 5 in female well-developed (Fig. 11); 1 functional spiracle in membrane at posterolateral



2 *Cryptochetum* 3 *Cryptochetum* 4 *Cryptochetum*

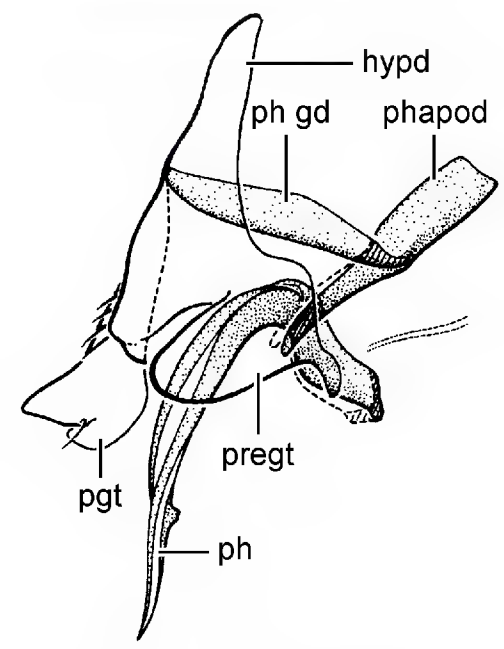


5 *Cryptochetum*



6 *Cryptochetum* ♂

7 *Cryptochetum* ♂



8 *Cryptochetum* ♂

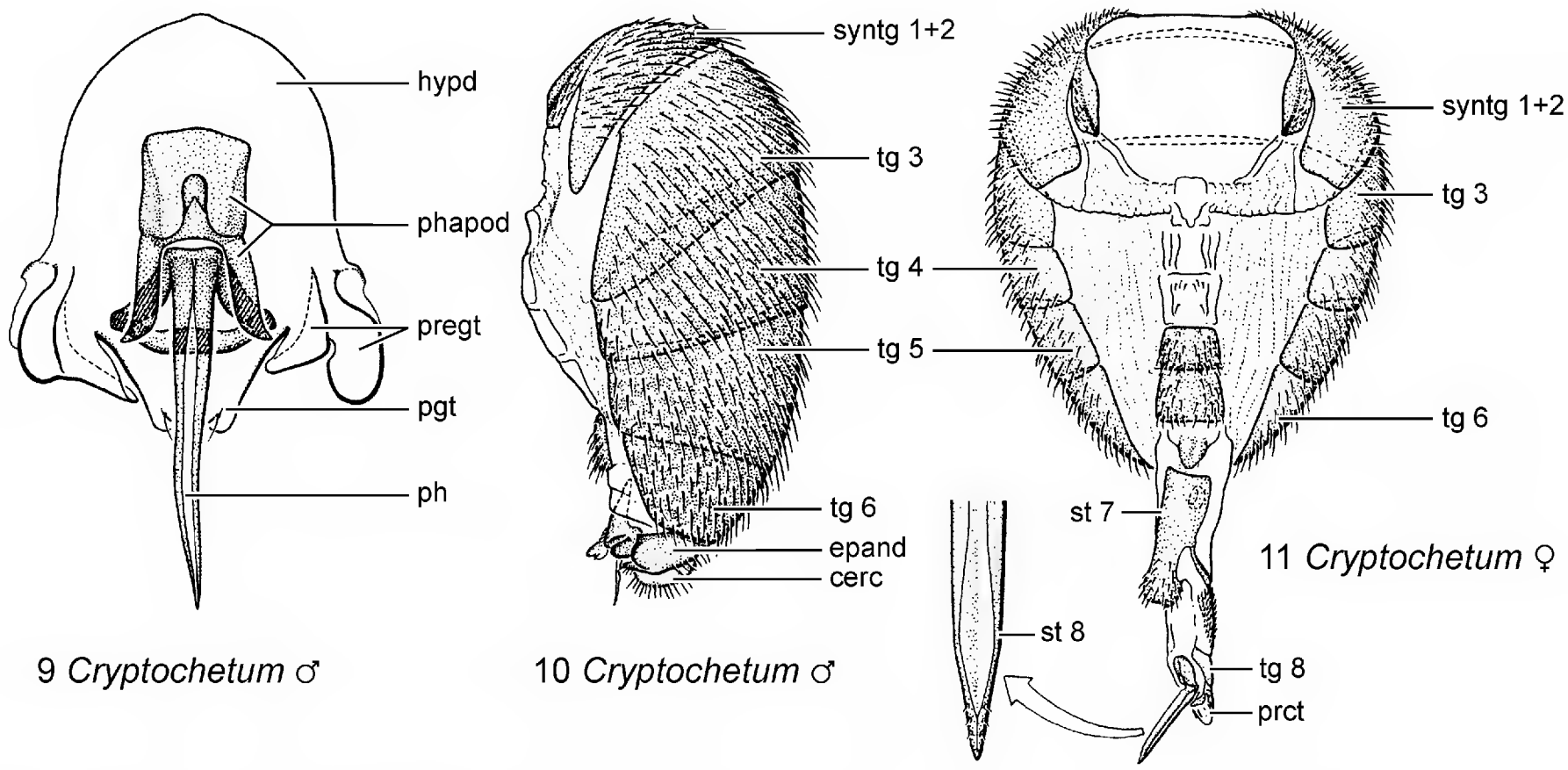
Figs 107.2–8. Heads, wing and male terminalia of Cryptochetidae: (2) head of *Cryprochetum* (*Atriangulum*) *capense* Van Bruggen, dorsal view; (3) same, *C.* (*Tritolestes*) *melan* Ghesquières; (4) same, *C.* (*Lestophonus*) sp.; (5) wing of *C.* (*T.*) *melan*, dorsal view; (6) male terminalia of *C.* (*L.*) *iceryae* (Williston), ventral view; (7) same, lateral view; (8) same, details of phallus and associated parts, lateral view. Figs 6–8 (McAlpine 1987, figs 2–4).

Abbreviations: A_1 – first branch of anal vein; *bm+dm* – basal medial cell + discal medial cell; *C* – costal vein; cerc – cercus; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *dm–m* – discal medial crossvein; ej apod – ejaculatory apodeme; epand – epandrium; *h* – humeral crossvein; hypd – hypandrium; M_1 – first branch of media; M_4 – fourth branch of media; oc tr – ocellar triangle; pgt – postgonite; ph – phallus; ph gd – phallic guide; phapod – phallapodeme; pregt – pregonite; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Sc* – subcostal vein; sur – surstylus.

margin of tergite 6; male postabdomen (Figs 6–9) with tergite 6 symmetrical; epandrium present as thin band dorsally, with a few setulae; surstylus fused to ventral extremities of epandrium, setulose at apex; cercus rather large; hypandrium U-shaped, open posteriorly; phallus C-shaped, long, slender and rigid; phallapodeme with 2 arms projected around base of phallus; ejaculatory apodeme fairly reduced; female with piercing ovipositor (Fig. 11, inset); female tergites 1 + 2–6 well-developed; female sternite 6 reduced and nodular; sternite 7 fairly unmodified, elongate and parallel-sided; sternite 8 highly modified; tergite 8 largely membranous, with spinulose dorsobasal region, posterior margin produced to form curved spine-like ovipositor; cercus reduced, fused medially to form an anus-bearing lobe projecting dorsally at base of ovipositor; 1 weakly sclerotised spermatheca present.

Egg (Fig. 12), elongate-oval, with apex narrower, broader at one end, with minute (easily detached), funnel-shaped micropyle; length *ca* 0.2 mm, width *ca* 0.1 mm; chorion surface unsculptured and smooth. Early first-instar larva lacking visible segmentation, sensory organs and cephaloskeleton; late first-instar larva (Fig. 13), with clearly segmented body and vestige of cephaloskeleton; 2 caudal filaments present on segment 8 (acting as tracheal gills), containing well-developed and visible nuclei of hypodermal cells (nutrition probably by diffusion through cuticle from hemolymph of host). Second-instar larva (Fig. 14), C-shaped, with fully formed tracheal trunks filled with air, but tracheal system closed (apneustic); body segmentation developed, consisting of pseudocephalon, prothorax, mesothorax, metathorax, plus 8 abdominal segments; prothoracic spiracles apparently absent; with single row of spicules present on metathorax and all abdominal segments with 4 similar rows; caudal filaments increase greatly in length as larva develops (larvae feed on hemolymph and fat body of host). Third-instar larva (Figs 15, 16), with ovoid-shaped body, with very long, or fairly short, caudal filaments; all body segments with multiple rows of spicules, but lacking demarcated creeping welts; cephaloskeleton, prothoracic and posterior spiracles developed; cephaloskeleton (Fig. 18), with basal sclerite spoon-shaped, dorsal cornu reduced, orientated vertically; intermediate sclerite somewhat club-shaped with two parallel bars; mouthhooks broad basally tapered to acute points; posterior spiracles protrudent, hook-like, in dorsal posterior region of abdominal segment 8 (used to puncture host cuticle at end of larval development, when connection with atmospheric air is established). Puparium (Fig. 17), ovoid, pointed at anterior end, rounded posteriorly; brownish black in colour, with demarcated segmentation and tail-like (easily detached) caudal filaments; operculum formed of 3 segments, line of dehiscence extending dorsally only, to form single detachable dorsal cap.

Cryptochetidae superficially resemble some Chloropidae (see Chapter 96) and share a number of characters, such as the enlarged ocellar triangle, the enlarged prosternum with precoxal bridge, the propleural carina, velvety sensorial macula on hind tibia and reduced and weakly sclerotised spermathecae. The wing venation, however, is more similar to the Milichiidae (see Chapter 95), with 2 costal breaks, the subcostal vein visible as a fold in membrane, presence of cell *cua* and clearly visible vein A_1. Cryptochetidae are easily separable from Chloropidae by the presence of clearly defined vein A_1 and from Milichiidae by the elongate, compressed postpedicel and (in the case of *Cryptochetum*), the complete lack of an arista.



Figs 107.9–11. Male terminalia and abdomens of Cryptochetidae: (9) male terminalia of *C.* (*L.*) *iceryae* (Williston), details of phallus and associated parts, ventral view; (10) same, male abdomen, lateral view; (11) same, female abdomen (inset: detail of ovipositor). Figs 9–11 (McAlpine 1987, figs 5–7).

Abbreviations: cerc – cercus; epand – epandrium; hypd – hypandrium; pgt – postgonite; ph – phallus; phapod – phallapodeme; prct – proctiger; pregt – pregonite; st – sternite; syntg – syntergite; tg – tergite.

Biology and immature stages

Larvae and development were studied in detail for *Cryptochetum iceryae* (Williston, 1888) and the non-Afrotropical *C. grandicorne* Rondani, 1875, by Thorpe (1930, 1934, respectively). Thorpe (1941*a*, *b*) provided descriptive details of immature stages for some Afrotropical species and Nartshuk (1979, 1981) published some information on non-Afrotropical species. Menon (1950) provided a general review of knowledge on the genus *Cryptochetum*.

Cryptochetum is strikingly poecilogonic (development in the same species with two larval forms, although adults appear alike) and in almost every species for which the life cycle is known, larvae provide more obvious specific characters than do the adults (Thorpe 1941*a*).

Larvae are endoparasitic on various scale insects of the subfamily Monophelebinae (Coccidae: Margarodidae) (Nartshuk 2000: 67) and larval stages occur within the host as solitary or gregarious parasites. Larvae are elaborately adapted to an endoparasitic mode of life in a particular host species and are characterised by strikingly long caudal filaments on abdominal segment 8 and partly reduced mouthparts. *Cryptochetum* species appear to be largely host-specific and Cadahia (1984) provided a tabulated list of *Cryptochetum* species and their known scale insect hosts. Thorpe (1930) suggested that it would not be surprising to find that every monophelebine scale insect in Africa has its own peculiar species of *Cryptochetum* associated with it.

Adults are slow-moving and can be found walking among colonies of scale insects, where they feed on honeydew (Evenhuis 1994: 452). When ready to oviposit, the female fly walks slowly over the potential host scale insects, moving her antennae slightly, but not actually touching and it is apparent that female flies are able to determine scales that already contain fly larvae in later stages of development and avoid these for oviposition (Thorpe 1930).

Eggs (Fig. 12) are deposited directly into the haemocoel of the host scale by use of the adapted spike-like ovipositor (Fig. 11). The egg stage lasts 3–5 days, during which it increases substantially in size, probably by absorbing water and food material from the body fluids of the host. All three larval instars occur within the host's body. The first-instar larva (Fig. 13) lacks mouthparts and apparently absorbs nutrients through the thin cuticle; it is incapable of movement and floats in the body fluids of the host scale. As eggs are laid more or less randomly, larvae occur in almost any part of the host's haemocoel. The duration of the first-instar larval stage is probably only 2 days. The immobile second-instar larva (Fig. 14) has a similar mode of life, except that liquid food is now absorbed orally, by use of a developed cephaloskeleton; the duration of this larval stage is probably 3–4 months. The third-instar larva is an ovoid-shaped maggot, tapered at both ends. The young third-instar (Fig. 15) has the caudal filaments extremely long, but as the column of air in the tracheoles begins to be withdrawn these filaments shrivel and are frequently broken-off near to base. The cephaloskeleton and sense organ are well-developed and the larva feeds indiscriminately on the body tissues of the host. During later developmental stages the larva makes contact with atmospheric air by piercing the host's cuticle with the spine-like posterior spiracles. The third-instar larval stage lasts about 10–12 days, during which feeding action reduces the host virtually to an empty skin. Pupariation takes place in the host with the posterior spiracles thrust through the body wall of the host; the puparial stage lasts about 6 months.

Economic significance

Adults of some *Cryptochetum* species are known to be highly obnoxious as "eye gnats" in Japan (*C. nipponense* (Tokunaga, 1945)), the Russian Far East (*C. smaragdinus* Séguy, 1948) (Nartshuk 1984: 67, 2000: 349), India and the Philippines (Foote & Arnaud 1958). No such cases have been recorded from the Afrotropical Region.

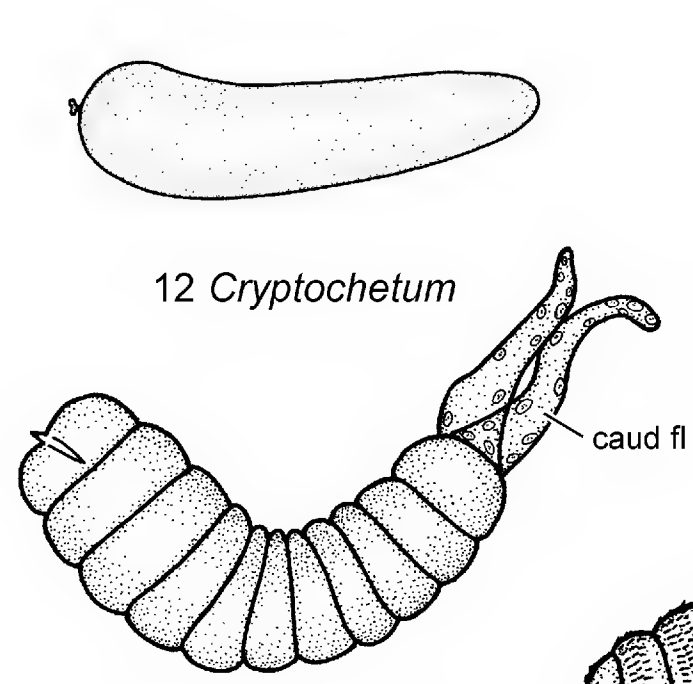
Two native Australian species of *Cryptochetum* were introduced into North America for the biological control of cushion scale pests on cultivated plants (Cadahia 1984; Cogan 1980: 691; Colless & McAlpine 1970: 730; Pitkin 1989: 666). *Cryptochetum iceryae* was introduced into California in 1888 (Thorpe 1934) to control Cottony cushion scale, *Icerya purchasi* Maskel (Coccidae: Margaroididae), a serious pest of citrus and *C. monophlebi* Skuse, 1889, a species associated with *Drosicha crawfordi* Maskel (Margaroididae) (Cadahia 1984), was introduced probably in the same year. Most authors (e.g., McAlpine 1987: 1069; McAlpine & Thompson 2011: 1123) record only *C. iceryae* as occurring in North America and Thorpe (1930) noted that it is likely that only *C. iceryae* became fully established. The remarkable efficiently of *Cryptochetum* in controlling cushion scale pests has been heralded as one of the most successful examples of biological control (McAlpine 1987: 1072; Nartshuk 2000: 352).

Cryptochetum iceryae was also apparently introduced into South Africa (first noted by Bezzi (1919)) for the same purpose, but South African records are doubtful. The species is, however, recorded from Democratic Republic of Congo, Rwanda and Uganda (Cogan 1980: 691; Van Bruggen 1960). Van Bruggen (1960: 288) further noted: "In 1959 a beginning was made to import *C. monophlebi* Skuse from Mauritius for the control of *Icerya seychellarum* (Westw.) on *Castanospermum australe* Cunn. (Leguminosae) in Pietermaritzburg, Natal …". *Cryptochetum monophlebi* is, however, native to Australia (Tasmania Is.) and is apparently not recorded from Mauritius Is., or elsewhere in the Afrotropics. This record probably represents a misidentification.

Classification

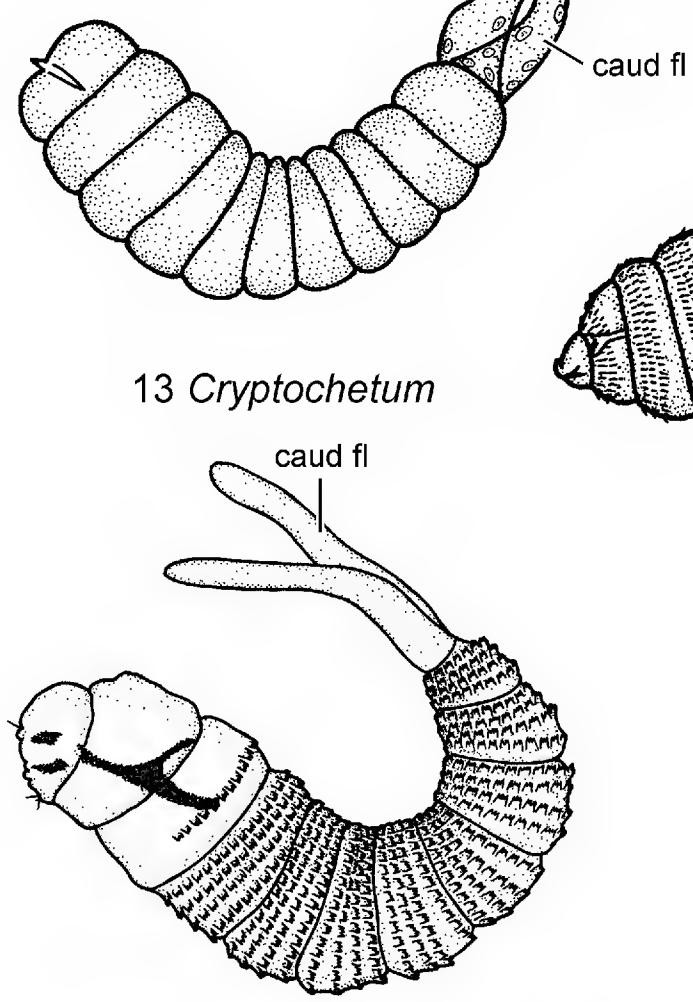
Two extant genera are included in the family, the native Old World genus *Cryptochetum* and the monotypic Australasian genus *Librella* (McAlpine 1976). Distribution of species of the family were mapped by Cadahia (1984, fig. 1) and more recently by Nartshuk (2000: 352, map 8.1).

One monotypic fossil genus, *Phanerochaetum* Hennig, has been described from Baltic amber of Eocene/Oligocene age (Hennig 1965, 1969), although following a review of characters and the phylogenetic position of the genus, McAlpine (1989: 1476–1478) postulated that it is more closely related to families in the superfamily Ephydroidea. Further studies of the type specimen are required to better ascertain its position among acalyptrate flies (Evenhuis 1994: 452).

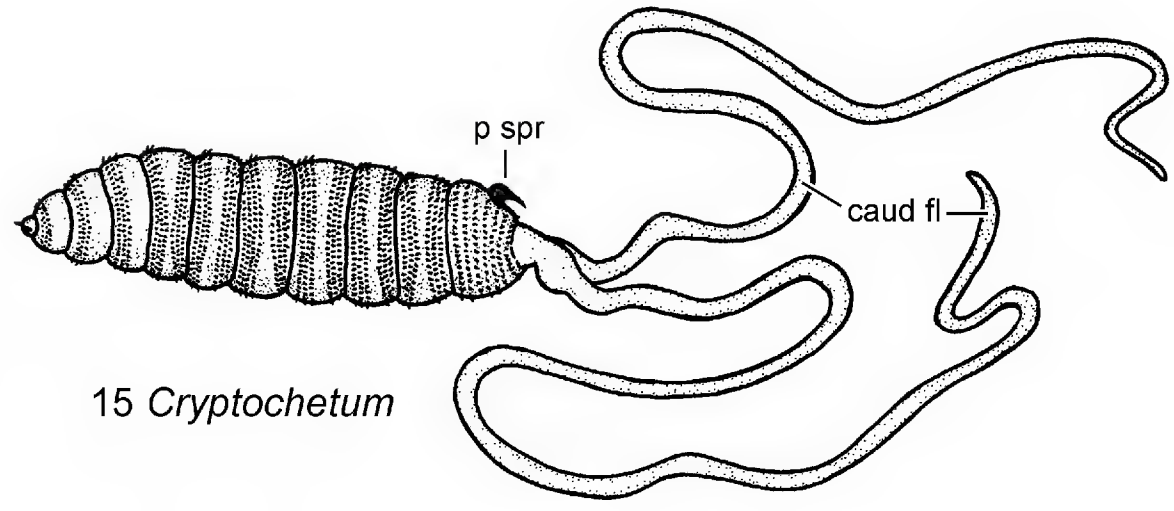


12 *Cryptochetum*

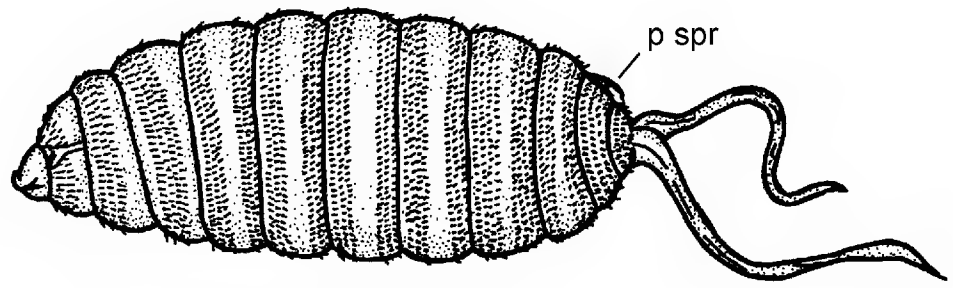
13 *Cryptochetum*



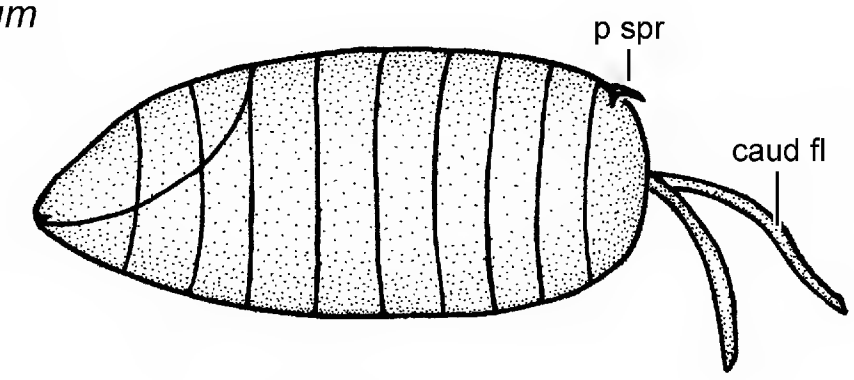
14 *Cryptochetum*



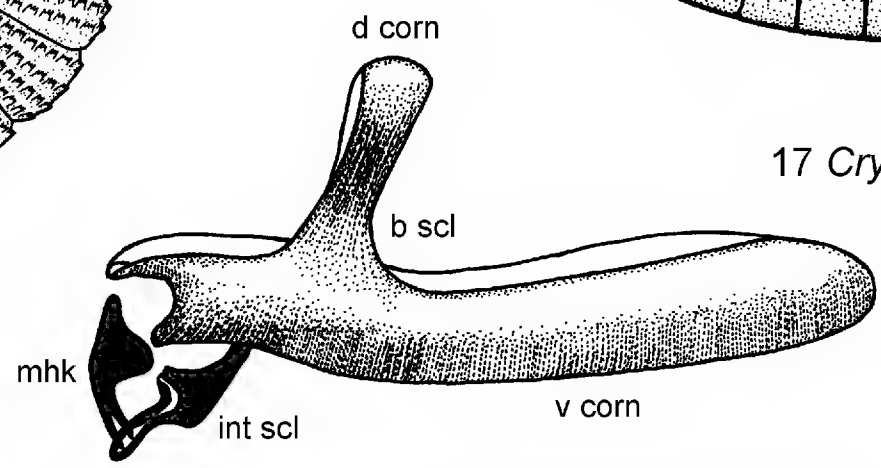
15 *Cryptochetum*

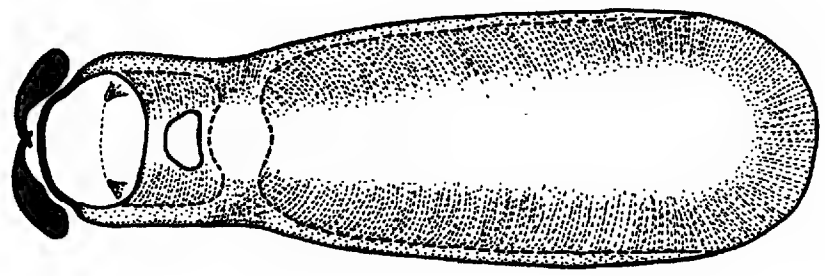


16 *Cryptochetum*



17 *Cryptochetum*





18 *Cryptochetum*

Figs 107.12–18. Egg, larvae, puparium and cephaloskeleton of Cryptochetidae: (12) egg of *Cryptochetum* (*s. str.*) *granadicorne* Rondani, lateral view (non-Afrotropical); (13) same, late first-instar larva, lateral view; (14) same, newly emerged second-instar larva, lateral view; (15) same, young third-instar larva, lateral view; (16) same, mature third-instar larva, lateral view; (17) same, puparium, lateral view; (18) same, cephaloskeleton, lateral view (above), dorsal view (below). Figs 12–18 (after Thorpe 1934, figs 5, 9, 12, 18, 20, 25, 21, 22, respectively).

Abbreviations: b scl – basal sclerite; caud fl – caudal filament; d corn – dorsal cornu; int scl – intermediate sclerite; mhk – mouth-hook; p spr – posterior spiracle; v corn – ventral cornu.

Cryptochetum has been assigned to various families in the past, including Agromyzidae, Carnidae, Chloropidae, Chamaemyiidae, Drosophilidae and Milichiidae (Nartshuk 2000: 352; Van Bruggen 1960). Brues & Melander (1932) resolved the uncertain placement of the genus by making a separate family for it. McAlpine (1989: 1476–1478) considers Cryptochetidae to be restricted to *Cryptochetum*, with the remaining two genera possibly belonging outside of the superfamily, with possible ties to Ephydroidea.

Hennig (1958) placed Cryptochetidae as a family of uncertain placement. He listed 13 synapomorphies in relation to the groundplan of the Schizophora and discussed evidence for a relationship with the superfamily Ephydroidea (as Drosophiloidea). Hennig (1969) connected the family doubtfully to the Milichioidea and later (Hennig 1973) considered it a family of uncertain placement. Griffiths (1972: 86) included the family in the superfamily Lonchaeoidea, together with Lonchaeidae, on the basis of the structure of the male terminalia and female ovipositor. McAlpine (1976) disagreed with Griffiths' (1972) interpretation and later McAlpine (1989: 1476) stressed relationships between the Chloropidae and Milichiidae (Nartshuk 2000: 352).

In a more recent molecular analysis that differs drastically from previous interpretations of superfamily relationships, Wiegmann *et al*. (2011) placed the Cryptochetidae in the superfamily Ephydroidea in a clade comprising Ephydridae, Drosophilidae, Cryptochetidae and Braulidae, with Cryptochetidae being sister-group to the Braulidae.

Identification

Checklists of world species of *Cryptochetum* were provided by Van Bruggen (1960) and Cadahia (1984) although these are now out of date. Afrotropical species were catalogued by Cogan (1980: 691–692).

Identification of adults is based entirely on external characters, especially wing venation, head shape and the shape and apical micro-setation of the postpedicel. Male terminalia (Figs 6–10) have not been sufficiently studied and many species are based on female types. No modern key to adults is currently available that includes all described Afrotropical species, but Thorpe (1941*a*) provided a key to the then known world species, excluding the two Afrotropical species subsequently described by Ghesquières (1943) and four South African species described by Van Bruggen (1960). Van Bruggen (1960) keyed species of the subgenus *Atriangulum* and Steyskal (1971) keyed the world species of the subgenus *Tritolestes* Ghesquières. A key to the third-instar larvae of eight world species was provided by Thorpe (1941*a*). Adults are frequently sampled in Malaise traps (A.H. Kirk-Spriggs, pers. obs.), often in large numbers and are normally micro-pinned in the field for later double-mounting (see Chapter 2)

Synopsis of the fauna

Only one genus, *Cryptochetum*, occurs in the Afrotropical Region.

***Cryptochetum* Rondani.** A genus of 28 described Old World species, native to the Afrotropical (13 recorded species; the largest regional fauna), Australasian (3), Oriental (7) and Palaearctic (6) Regions. The genus is not native to the New World, but one species, *C. iceryae* was introduced into North America for the biological control of Monophlebinae coccids (see above). The genus occurs mainly in the tropical and sub-tropical zones, especially in savanna habitats and is divided into four poorly defined subgenera: *Atriangulum* Van Bruggen (2 Afrotropical species), *Cryptochetum sensu stricto* (0), *Lestophonus* Williston (7) and *Tritolestes* Ghesquières (4), based entirely on characters of the ocellar triangle; a key to these subgenera was provided by Van Bruggen (1960). These subgenera are weak at best, there is no phylogenetic support for their retention and they would be better treated as informal species-groups or complexes. Most Afrotropical species are only known from the type locality, but the genus is widespread in the Afrotropical Region and unstudied material is available in African museums from Angola, Cameroon, Democratic Republic of Congo, Kenya, Malawi, Madagascar, Mauritius Is., Zambia, and most abundantly from Namibia and South Africa. Additional new species are expected following revisionary work and further rearing from their Monophlebinae hosts.

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TAXONOMIC INDEX TO VOLUME 3

Ashley H. Kirk-Spriggs

This index is restricted to the taxonomic names associated with Diptera that appear in Volume 3 of this *Manual*. Similar names of plants and animals other than Diptera are excluded. Bibliographical references are not indexed. Non-Afrotropical taxon names are also listed.

Taxonomic names are provided for all taxonomic ranks below order level (*i*.e., series, subfamilies, superfamilies, tribes, genera, subgenera, species and subspecies). Other major divisions, such as lower Brachycera and orthorrhaphous Brachycera, are also indexed. Family name citations are only indexed for the first page of each family chapter (underlined), but all references to family names in other chapters are indexed separately. In the case of "Undescribed genera", as cited in the text, these are listed followed by the respective family name in parenthesis.

Taxonomic names of ranks above genus level are provided in upper case Roman font and genus, species and subspecies names in *italic* font (including synonyms). If a text citation, illustration and/or family key citation appear on the same page, the page number is repeated in the order in which they appear. Authors' names are provided for genus, species and subspecies names and in such cases these names are followed by the names of the genera to which they are assigned. Subgeneric names are indexed in the same way as generic names and subspecific names in the same way as specific names. **Boldface** page numbers indicate where names appear in the identification keys; underlined page numbers indicate where a genus name appears in the "Synopsis of the fauna" section of each family chapter; *italicised* numbers indicate the location of illustrations of these taxa.

A complete index of taxonomic names of Diptera is included in Volume 4.

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SURICATA

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True flies, or **Diptera**, constitute one of the largest orders of insects in the biosphere, with over 160,000 described species worldwide, more than 20,000 of which occur in the Afrotropical Region. They are as diverse morphologically and biologically as they are numerous and many groups have evolved spectacular structural adaptations that are commensurate with their environment and biology. During their long evolutionary history, virtually every terrestrial niche has been occupied by the Diptera, making them one of the most successful groups of organisms on Earth. Many have co-evolved in association with other organisms and become highly specialised parasites or parasitoids of a range of disparate groups of plants and animals. Whether focusing on their systematics, biology, biogeography, conservation, or the more applied aspects, the Diptera remain a fascinating and intriguing group. This four volume book, a collaboration of **over 90 international experts** on Diptera, is the first-ever synopsis of the **108 families** of flies known from the Afrotropical Region and includes discussions on biology and immature stages, economic importance, classification, identification to the genus level, as well as a synopsis of each genus. This work provides the basics for understanding the diversity of a major order of insects in a large tropical and sub-tropical region and is the first such synopsis of its kind for any major insect order occurring in the Afrotropics.

Volume 3 includes **family chapters** dealing with **51** of the 108 families of flies that occur in the region and covers the Brachycera: Cyclorrhapha, excluding Calyptratae (sometimes termed the higher Diptera). Each chapter includes a diagnosis of the family, sections dealing with biology and immature stages, classification and identification, an identification key to genera (if more than one) and a synopsis of the fauna section, arranged genus by genus alphabetically. The text is richly illustrated with over **3,447 illustrations**, including **1,746 colour** and **101 black and white images** and **1,600 line drawings** of flies.

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